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# Digestive physiology of the the plains viscacha (*Lagostomus maximus*) in comparison with other rodents, rabbits and horses

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## Digestive physiology of the the plains viscacha (*Lagostomus maximus*) in comparison with other rodents, rabbits and horses

Viscachas (*Lagostomus maximus*) are herbivorous rodents native to South America. In three different experiments with a total of 16 adult animals and 6 different diets (total n of feeding trials = 35; not all measurements taken in all trials), various aspects of the digestive physiology of viscachas were investigated. First, a new dataset on dietary crude fibre, macromineral composition and the apparent digestibility of organic matter and macrominerals in rabbits (a total of 180 measurments with 12 individuals and 10 different diets) was added to literature data for rabbits, rodents and domestic horses, as a basis for comparison with viscachas. Viscachas achieved digesta retention times similar to that of horses; these did not differ for solute or small particle markers. Secondary marker excretion peaks indicated coprophagy, and were rarer on high-protein diets. Resting metabolic rate was lower than expected for mammals of this size at 229 kJ $kg^{-0.75}$ $d^{-1}$. On diets including concentrate feeds, viscachas excreted glucose in their urine. The data indicate similarities in the digestion of protein, lipids and macrominerals (in particuar, calcium) between hindgut fermenting herbivores irrespective of the strategy of coprophagy. With respect to a digestibility-reducing effect of dietary fibre, viscachas differed from rabbits and guinea pigs but were similar to horses, corroborating that small body size need not necessarily be linked to lower digestive efficiency on high-fibre diets.

*Keywords:* herbivore, rodent, digestive physiology, calcium, fossoriality, coprophagy

## Die Verdauungsphysiologie vom Flachlandviscacha (*Lagostomus maximus*) im Vergleich zu anderen Nagern, Kaninchen und Pferden

Viscachas (*Lagostomus maximus*) sind herbivore südamerikanische Nager. In drei Versuchen mit insgesamt 16 adulten Tieren und 6 verschiedenen Rationen (insgesamt 35 Fütterungsversuche; nicht alle Daten in allen Versuchen erhoben) wurden Aspekte ihrer Verdauungsphysiologie untersucht. Zuerst wurde ein neuer Kaninchen-Datensatz zu Rohfaser, Mineralgehalt und der scheinbaren Verdaulichkeit von organischer Substanz und Mineralstoffen (insgesamt 180 Messungen mit 12 Tieren und 10 Rationen) einer Literatur-Datensammlung für Kaninchen, Nagern und Pferden hinzugefügt, als Vergleichsbasis für die Viscachas. Viscachas erreichen Retentionszeiten wie Pferde, ohne Unterschied zwischen löslichem und partikulärem Marker. Sekundäre Marker-Peaks zeigten Koprophagie an, und waren seltener auf proteinreichen Rationen. Mit 229 kJ $kg^{-0.75}$ $d^{-1}$ war der Ruheumsatz niedriger als bei einem Säuger dieser Grösse erwartet. Auf Rationen mit Konzentratfutter schieden die Viscachas Glukose im Urin aus. Die Daten weisen auf Gemeinsamkeiten in der Verdauung von Protein, Fett und Mineralien (insbesondere Kalzium) bei Dickdarmfermentierern hin, unabhängig davon, ob Koprophagie Bestandteil ihrer Verdauungsstrategie ist oder nicht. Hinsichtlich einer Verringerung der Verdaulichkeit durch Rohfaser waren Viscachas anders als Kaninchen und Meerschweinchen, ähnelten aber Pferden. Dies belegt, dass kleine Tiere fasserreiche Nahrung nicht notwendigerweise aufgrund ihrer Körpergrösse schlechter verdauen müssen.

*Stichworte:* Pflanzenfresser, Nager, Verdauungsphysiology, Kalzium, unterirdische Lebensweise, Koprophagie

# 3. Introduction

This study investigates the species-specific digestive physiology of viscachas. In order to establish a database with which the viscacha data could be compared, a new dataset on dietary crude fibre, macromineral composition and the apparent digestibility of organic matter and macrominerals in rabbits was added to literature data for rabbits, rodents and domestic horses. Therefore we divided every section of the monography in two parts, the first part focusing on developing this database, the second concentrating on the viscacha.

## *3.1 Organic matter and macromineral digestibility of domestic rabbits compared to other hindgut fermenters*

Animal species differ in many physiological characteristics. Comparing sets of species with respect to these characteristics is the aim of comparative physiology. However, due to the logistics of animal husbandry and experiment realisation, the comparative data is often not generated in a single, comprehensive multi-species experiment, but is collated from many individual studies. Typical examples are investigations on factors that influence mammalian metabolic rate, which collate data from a large number of sources (McNab 2008; Sieg et al. 2009; Müller et al. 2012). The situation is similar in digestive physiology, where single studies on comprehensive species sets are rare (Foose 1982; Steuer et al. 2011; Clauss et al. 2015) and comparative evaluations are mostly based on datasets collated from a multitude of studies (Müller et al. 2011; Müller et al. 2013). An interesting question is whether species differences that can be demonstrated in individual experiments, during which the same husbandry conditions and dietary regimes are used for all investigated species, are also reflected in data collected from a multitude of sources.

The digestive efficiency of herbivores is a typical example. In individual studies, with identical conditions, it could be shown that rabbits (*Oryctolagus cuniculus*) generally achieve lower digestive efficiencies than guinea pigs (*Cavia porcellus*) (Slade and Hintz 1969; Sakaguchi et al. 1987; Sakaguchi et al. 1992a; Schwabe 1995; Franz et al. 2011a), chinchillas (*Chinchilla laniger*) (Wenger 1997) or degus (*Octodon degus*) (Hommel 2012), that guinea pigs achieve higher digestive efficiencies than chinchillas (Wenger 1997), or that digestive efficiency is higher in horses as compared to rabbits but similar to guinea pigs (Slade and Hintz 1969; Udén and Van Soest 1982). Whether these differences can be demonstrated in larger data collections that combine data from such individual studies remains to be tested.

Another example is the apparent digestibility (aD) of minerals. While it is, for example, assumed that sodium absorption from the gut is quite uniform across mammals, with a very

high true digestibility (Robbins 1993), there is large variation in the aD of calcium across species. Many species excrete calcium mainly via faeces, such as rats (Hansard and Crowder 1957; Cheeke and Amberg 1973), pigs (Hansard et al. 1961) and domestic ruminants (Khorasani et al. 1997; Martz et al. 1999). In contrast, many hindgut fermenters absorb calcium from the gut in amounts that exceed requirements, and eliminate the surplus via urine. This has been demonstrated in horses (Schryver et al. 1974), rabbits (Chapin and Smith 1967; Cheeke and Amberg 1973; Kamphues et al. 1986), or guinea pigs (O'Dell et al. 1957; Meyer et al. 1996a). To which degree species comparisons can be made not only at a qualitative but also at a quantitative level has so far rarely been investigated.

The aim of this study was to establish relationships between dietary crude fibre content and the apparent digestibility of organic matter in rabbits, and to compare the obtained results to previously published data for rabbits and other small hindgut fermenters and horses. In particular, we wanted to test whether differences evident in individual species comparisons remain evident in literature data collections. Additionally, we aimed at establishing relationships between mineral and digestible mineral content in rabbits and at comparing the results to those previously published in rabbits and other hindgut fermenters.

### *3.2 Digestive physiology of the plains viscacha compared to other hindgut fermenters*

In the debate on the influence of body size on digestive physiology, niche differentiation and species diversification, the traditional focus has been on large ungulate herbivores with well-documented differences in diet type and diet quality (Clauss et al. 2013). Efficient herbivory has long been considered a privilege of large-bodied mammals (Demment and Van Soest 1985; Foley and Cork 1992), and herbivorous small mammals such as rodents appear less intensively studied (Smith 1995). However, many rodent species are true herbivores (Wilman et al. 2014) with a variety of corresponding morphological and physiological adaptations (Gorgas 1966; Cork et al. 1999; Sakaguchi 2003) that need to be understood for a full assessment of strategies facilitating herbivory. These adaptations comprise selective feeding (Justice and Smith 1992), a strategy of compensatory high food intake as diet quality declines (Meyer et al. 2010), relative gut capacities similar to those of larger mammals, digesta retention times that are similar to, or lower than, those of larger mammals (Müller et al. 2013), different strategies with respect to the movement of fluids and particles in the colonic separation mechanism that facilitates the strategy of coprophagy (Hume and Sakaguchi 1991; Franz et al. 2011a), microbial fibre fermentation (Stevens and Hume 1998), a strategy to absorb more calcium than required from the intestinal tract and excrete the surplus via urine

(Clauss and Hummel 2008), and a relative methane production similar to other nonruminant mammals (Franz et al. 2011b).

Plains viscachas (*Lagostomus maximus*) are hystricomorph South American rodents that occur in a variety of arid, semiarid or humid habitats; they are colonial and live in a communal burrow system (Jackson et al. 1996). Plains viscachas are herbivorous (Campos et al. 2001), with an apparent preference for grasses (Giulietti and Jackson 1986; Branch et al. 1994; Puig et al. 1998; Bontti et al. 1999; Pereira et al. 2003), have a colonic furrow typical for hystricomorph rodents (Gorgas 1966) and practice coprophagy (Jackson et al. 1996; Clauss et al. 2007a). They have been reported to have a low metabolic rate and the ability to concentrate urine similar to desert rodents (Kohl 1980). Plains viscachas are particularly susceptible to diet-induced diabetes mellitus with cataract formation when kept on energy-dense diets in captivity, similar to degus (*Octodon degus*) (Rübel et al. 1989; Gull et al. 2009; Wenker et al. 2009). In the course of investigating the nutritional requirements of this species, the various experiments reported in this study were performed, facilitating a comparison of the plains viscacha with other herbivores, to assess convergence or homology in digestive function, and in particular to test, in a comparison with domestic horses, whether differences in the digestive efficiency either putatively related to body mass (the influence of dietary fibre on digestive efficiency) or to digestive strategy (assuming higher apparent digestive efficiency for protein and lipids in coprophagous vs. a noncoprophagous herbivore) can be demonstrated.

# 4. Animals, Materials and Methods

### *4.1 Domestic rabbits and other hindgut fermenters*

This experiment was approved by Animal Care and Use Committee of the Veterinary Office of Zurich (Nr. 114/2008). The experiment, including housing details, has been described in detail by Tschudin et al. (2011b). Twelve adult dwarf rabbits were used to assess ten different diets; each animal received five diets in sixteen treatments (with each diet assessed with water provided via nipple drinker and via open dish, and one diet additionally during a drinker choice experiment (Tschudin et al. 2011a) and at two levels of water intake restriction). Each treatment lasted 15 days. The order of the treatments was randomized to exclude environmental influences. The treatments were calculated for the actual or target body mass with respect to the daily digestible energy (DE) requirement (440kJ DE kg $BM^{-0.75}$; Kamphues et al. 2009). The nutrient composition of the individual ingredients items (Table 1) used in the various diets are given in Tschudin et al. (2011b). All animals were offered hay ad libitum and expected to consume it to meet their overall requirements. After 11 days of acclimatization to a new diet, rabbits were placed in metabolism cages, where food intake and faecal output were measured for four consecutive days. Diet items were sampled representatively, and leftovers and faeces were collected quantitatively and stored at -21°C. Only in the case of two pelleted diets were leftovers not submitted to subsequent analysis, as selective feeding was not possible with these items.

Samples of feed, leftovers and faeces were dried to constant weight at 60°C and ground (1mm, Retsch Mühle, Retsch GmbH, Haan, Germany). Samples were analysed for dry matter (DM) and total ash; feed and leftovers were additionally analysed for crude protein and crude fibre (CF) (AOAC 1995), and neutral and acid detergent fibre (Van Soest et al. 1991, values corrected for residual ash). All samples were additionally tested for sodium (Na), potassium (K), calcium (Ca), phosphorus (P), and magnesium (Mg), using the crude ash residue as base material. The residue was dissolved in 10ml 8% hydrochloric acid, centrifuged at 20°C and 1590g for 20 min, and the supernatant was analysed by Cobas Miro Analysenautomat (Roche, Basle, Switzerland) for Ca, P and Mg, and by flame photometry (Flame Photometer 243, IG AG Zurich, Switzerland) for Na and K. Organic matter (OM) was calculated as 100 – total ash. Dietary fibre and mineral contents were calculated accounting for leftovers. Apparent digestibilities (aD) of OM and minerals were calculated as the percentage not excreted of the overall dietary intake.

Comparative data were collected from the literature (as indicated in the respective figure legends). Data were analysed using linear regression analysis; the 95% confidence interval of parameter estimates is given [in brackets]. In the case of the rabbit data from the present study, the individual was included as a random factor in linear mixed models. Additionally, various effects on apparent mineral digestibility from the present study were assessed using linear mixed models with the dietary concentration of digestible mineral as the dependent variable, the dietary concentration of crude minerals as independent variables, the individuum as random factor, and several other measures (e.g. the proportion of hay, parsley or nonforage components of the overall dry matter intake, or concentrations of other minerals or fibre fractions) as covariables. Models were compared for goodness-of-fit using Akaike's Information Criterion (AIC; lower values indicate a model that is more supported), aware that models that differ in AIC score by less than 2 should be considered equally supported (Burnham and Anderson 2001; 2002). Statistical tests were performed in R 2.15.0 (R Core Team 2012) using the package nlme , using the maximum likelihood function for the random factor (Pinheiro et al. 2011).

### *4.2 Plains viscacha*

Four adult plains viscachas (Table 2.1) euthanized at a zoological facility for management reasons were available to document the macro anatomy of the digestive tract. Animals were weighed, their body length recorded (as the distance from snout to the base of the tail), the digestive tract was dissected, freed from mesenteries, and the length and masses of individual gut sections and their contents were measured.

Between 2003 and 2013, three different feeding experiments (Exp1-3) were performed for this study. Exp1 was performed with 7 adult plains viscachas undergoing two dietary treatments, consisting of a grass hay-only diet (Exp1A) and a diet where grass hay was supplemented with a commercial pelleted food and carrots (Exp1B) (Table 2.2). Exp2 was performed with 6 adult viscachas undergoing three dietary treatments, consisting of two grass hay-only diets (Exp2A and C) and a diet where grass hay was supplemented with a different commercial pelleted food in between (Exp2B). Exp3 was performed with 3 adult viscachas fed a diet of lucerne hay and lucerne pellets.

Experiments included adaptation periods to the respective diets of 7 days (Exp1), 8 weeks (Exp2) or 14 days (Exp3); animals were housed individually in various enclosure types provided with a den-like shelter and water ad libitum. In Exp1 and Exp3, adaptation periods and collection periods were performed in the same enclosures (1.2-2.0 $m^2$, at ambient

temperatures of 20-22°C). In Exp2, to facilitate urine collection, animals were transferred to cages (0.35-0.58 $m^2$) with a mesh floor for the last days of adaptation and the collection periods (at ambient temperatures of 5-15°C). Collection periods lasted for a minimum of five days. Food intake was quantified by weighing food offered and leftover, and faecal output was quantified by total faecal collection. Due to the visual impression that individual faecal pellets were distinctively smaller in Exp2B than previously in Exp2A, ten randomly selected individual faecal pellets were weighed per animal in Exp2B and C. In Exp2, water intake was quantified by weighing water offered and left (accounting for evaporation losses using a control dish), and urine was collected completely from a funnel system attached underneath the wire mesh cages and the finer mesh where faeces were caught.

Representative pooled samples of feeds and faeces were taken for analysis. When sampling faeces, those faecal pellets evidently contaminated by urine were discarded. The composition of leftover hay was only analysed in Exp2 and Exp3. Samples were submitted to standard nutrient analyses (AOAC 1995) in duplicate for dry matter (DM) and total ash (AOAC no. 942.05), crude protein (AOAC no. 977.02), ether extract (AOAC no. 963.15), crude fibre (AOAC no. 930.10) as well as neutral detergent fibre ($NDF_{OM}$, AOAC no. 2002.04), acid detergent fibre ($ADF_{OM}$) and acid detergent lignin analysis (AOAC no. 973.18). All fibre values are expressed without residual ash. Organic matter was calculated as 100-total ash. Gross energy (GE) was determined by bomb calorimetry (IKA-Calorimeter C4000, Ika, Stauffen, Germany). Concentrations of sodium (Na), potassium (K), calcium (Ca), phosphorus (P), magnesium (Mg), copper (Cu) and zinc (Zn) were analysed in Exp1 and 2. To 0.5 g of sample, 5 ml of 65% $HNO_3$ was added for wet ashing (1200 mega High Performance Microwave, MLS, Milestone, Leutkirch, Germany). Ca, Na and K were analysed by flame photometry (EFOX 5053, Eppendorf, Hamburg, Germany), P by spectrophotometry (using ammonium molybdic acid and ammonium vanadic acid, 1:1; GENESYS 10 UV, Thermo Spectronic, Dreieich, Germany), and Cu and Zn by atomic absorption spectroscopy (AAnalyst 800, Perkin-Elmer, Waltham, MA, USA). Metabolic faecal nitrogen was determined in Exp1 according to Schwarm et al. (2009). Apparent digestibilities were calculated as the proportion of a nutrient not excreted of the overall intake (Robbins 1993). To facilitate comparison with data from other species, the concentration of a nutrient was plotted against the concentration of the digestible fraction of that nutrient (Clauss et al. 2008; Clauss et al. 2010b).

The mean retention time (MRT) of a solute marker (cobalt-EDTA) and a particle marker (chromium-mordanted fibre particles <2mm) prepared according to Udén et al. (1980) was

measured in Exp1A/B, Exp2A and Exp3, as described previously for two individual animals of Exp1A by Clauss et al. (2007a), feeding markers as a pulse-dose and sampling faeces at regular intervals afterwards. Faeces were analysed for markers either using the atomic absorption spectroscopy as described by Behrend et al. (2004; Exp1 and 2) or inductively coupled plasma optical emission spectrometry as described by Frei et al. (2015; Exp3). The mean retention time through the whole digestive tract (MRT) was calculated according to Thielemans *et al*. (1978) as

$$MRT = \frac{\Sigma\, t_i\, C_i\, dt_i}{\Sigma\, C_i\, dt_i}$$

with $C_i$ = marker concentration in the fecal samples from the interval represented by time $t_i$ (h after marker administration, using the midpoint of the sampling interval) and $dt_i$ = the interval (h) of the respective sample

$$dt_i = \frac{(t_{i+1}-t_i)+(t_i-t_{i-1})}{2}$$

The marker was assumed to have been excreted completely once the fecal marker concentrations were similar to the background-levels determined in pre-dose fecal samples.
Urine samples were available from spontaneous urinations or urine gained by applying gentle transabdominal pressure on the bladder under isoflurane anaesthesia (Wenker et al. 2007) at the end of each collection period in Exp1, or from total collection in Exp2. Urinary glucose concentration was estimated with a commercial test strip (Combur-Test, Roche Diagnostics AG, Rotkreuz, Switzerland; graded at 1 = below detection limit, 2 = 2.8, 3 = 5.6, 4 = 16.7 and 5 = 55.5 mmol $l^{-1}$). Blood samples were taken under isoflurane anaesthesia at the end of each collection period in Exp1 and 2 from the *Vena femoralis* and centrifuged to gain serum, which was analysed for glucose and fructosamin concentrations in a Cobas-Integra 700 Analyzer (Roche-Diagnostics, Rotkreuz, Switzerland). Additionally, urinary glucose was measured in Exp2B/C using the same equipment.

Subsequently to the collection period, the three animals of Exp3 were transferred to respiration chambers (0.12 $m^3$) that had served as shelter in their enclosures during the preceding trial periods. Chambers were filled with ad libitum amounts of lucerne hay, lucerne pellets and water. Air inlets on the bottom and air outlets on top of the chambers ensured a constant airflow (10 l $min^{-1}$) generated by an attached pump (Flowkit 100, Sable Systems, Las Vegas, USA). Flexible hoses ducted the out-flowing air to a gas multiplexer, which allowed

the simultaneous measurement of data on three individuals and as well as ambient air to determine base line gas values, at alternating intervals of 90 s each. Concentrations of $O_2$ and $CO_2$ were analysed by a Turbofox (Sable Systems). Methane was measured by a MA-10 Methane Analyser (Sable Systems). Data were adjusted for barometric pressure, water vapour pressure and air flow rates, which were constantly recorded during respirometry (Turbofox, Sable Systems). Gas analysers were manually calibrated with calibration gases (pure $N_2$, and a mixture containing 19.91 % $O_2$, 0.5032 % $CO_2$, 0.4945 % $CH_4$ dissolved in $N_2$). Data obtained by the respirometry system were analysed with the software ExpeData (Sable Systems) for $O_2$ consumed and $CH_4$ and $CO_2$ emitted after correcting for gas concentrations in incoming air. The mean metabolic rate (MR) was calculated based on the entire 23-h measurement period, therefore accounting for the activity of the animals inside the box, while the resting MR (RMR) of the animals was calculated by selecting the 20 lowest $O_2$ measurements per individual within the entire measurement (adapted from Derno et al. 2005). Data from the first hour the animals spent inside the respiration chambers were neglected. In order to estimate MR we multiplied the amount of $O_2$ consumed (in l $h^{-1}$) by 20.08 kJ (McNab 2008).

For comparative purposes, data collected in chapter 4.1 were used. Data were analysed, as appropriate, by parametric or nonparametric tests for paired measurements, using Sidak correction for multiple testing when indicated. Analyses were performed in SPSS 21.0 (SPSS Inc., Chicago, IL), with the significance level set to 0.05.

# 5 Results

## *5.1 Organic matter and macromineral digestibility of domestic rabbits compared to other hindgut fermenters*

### *5.1.1 Own measurements*

The nutrient and mineral composition of the actually consumed diets are indicated in Table 1.1. Generally, rabbits consumed higher proportions of hay than intended during diet calculation. The relative dry matter intake increased on diets with increasing crude fibre content (Fig. 1.1A; Table 1.2). There was a clear negative relationship between dietary CF and aD OM (Fig. 1.1B). Whereas the concentration of digestible Na and K appeared as clear functions of the respective crude mineral concentration (Fig. 1.2AB), this relationship appeared less strict for Ca (Fig. 1.2C), and absent for P and Mg (Fig. 1.2DE). In all cases, AIC values were lower in models that included the individuum as a random effect (Table 1.3). Models that only related digestible mineral content to the crude content of the respective mineral were always less supported than models that included additional factors, such as the content of other minerals, diet descriptors, or fibre levels (Table 1.3); however, many models with several such factors were equally supported, and there was no typical set of factors that were consistently present in the best-supported models (Table 1.3).

**Table 1.1.** Ingredient and nutrient composition of the diets actually consumed by rabbits in this study

| Diet | n | Hay | Parsley | Pellets/ Grains | TA | CP | CF | $NDF_{OM}$ | $ADF_{OM}$ | Na | K | Ca | P | Mg |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | % dry matter intake | | | g/kg dry matter | | | | | | | | | |
| Hay100[a] | 12 | 100 | 0 | 0 | 101.3 ±0.1 | 119.9 ±0.0 | 256.4 ±0.0 | 596.3 ±0.1 | 299.4 ±0.1 | 0.30 ±0.00 | 22.68 ±0.00 | 7.46 ±0.04 | 2.00 ±0.00 | 1.05 ±0.01 |
| HRP90[b] | 12 | 40 ±4 | 0 | 60 ±4 | 93.0 ±0.5 | 117.7 ±0.1 | 266.2 ±0.6 | 574.1 ±1.4 | 315.6 ±1.0 | 1.91 ±0.10 | 18.64 ±0.26 | 6.04 ±0.09 | 2.06 ±0.00 | 0.92 ±0.01 |
| Pellet90[b] | 12 | 21 ±9 | 0 | 79 ±9 | 78.8 ±2.7 | 150.5 ±3.7 | 188.0 ±8.2 | 427.1 ±20.4 | 243.6 ±6.7 | 3.52 ±0.39 | 11.40 ±1.72 | 6.07 ±0.15 | 3.10 ±0.13 | 0.88 ±0.02 |
| Parsley90[c] | 12 | 52 ±8 | 48 ±8 | 0 | 125.9 ±4.1 | 151.0 ±5.1 | 193.2 ±10.4 | 420.1 ±28.9 | 252.6 ±7.7 | 1.75 ±0.24 | 36.07 ±2.19 | 8.63 ±0.22 | 2.39 ±0.06 | 0.96 ±0.01 |
| Parsley50[c] | 12 | 73 ±3 | 27 ±3 | 0 | 115.2 ±1.7 | 137.6 ±2.1 | 220.5 ±4.2 | 496.1 ±11.8 | 272.8 ±3.1 | 1.12 ±0.10 | 30.30 ±0.90 | 8.10 ±0.09 | 2.22 ±0.03 | 0.99 ±0.01 |
| SeedParsley45[d] | 12 | 23 ±13 | 32 ±7 | 44 ±6 | 105.0 ±2.0 | 137.5 ±3.8 | 147.0 ±17.8 | 370.4 ±38.5 | 199.4 ±15.8 | 2.47 ±0.36 | 25.09 ±1.09 | 9.58 ±0.38 | 3.19 ±0.18 | 0.80 ±0.03 |
| SeedParsley33[d] | 42 | 50 ±6 | 20 ±3 | 30 ±4 | 102.8 ±0.9 | 130.5 ±1.5 | 185.5 ±8.5 | 451.7 ±17.5 | 234.1 ±7.8 | 1.70 ±0.17 | 23.77 ±0.48 | 8.80 ±0.19 | 2.78 ±0.09 | 0.88 ±0.02 |
| Seed70Parsley20[e] | 12 | 28 ±12 | 15 ±6 | 57 ±10 | 92.1 ±3.8 | 125.1 ±3.9 | 150.3 ±18.8 | 403.2 ±37.2 | 196.1 ±17.8 | 2.29 ±0.36 | 18.18 ±1.99 | 9.53 ±0.38 | 3.32 ±0.22 | 0.77 ±0.04 |
| Seed50[f] | 42 | 45 ±15 | 0 | 55 ±15 | 85.4 ±4.1 | 115.8 ±1.1 | 172.9 ±22.0 | 462.0 ±35.4 | 213.8 ±22.6 | 1.79 ±0.39 | 14.47 ±2.17 | 9.13 ±0.46 | 3.16 ±0.31 | 0.82 ±0.06 |
| Seed90[f] | 12 | 24 ±14 | 0 | 76 ±14 | 79.5 ±3.8 | 114.3 ±1.0 | 142.0 ±20.5 | 412.3 ±33.0 | 182.1 ±21.0 | 2.34 ±0.37 | 11.43 ±2.02 | 9.74 ±0.44 | 3.59 ±0.28 | 0.73 ±0.05 |

Planned diets: [a]grass hay ad libitum, [b]Healthy Rabbit Pro or Laboratory rabbits pellets 90%, [c]fresh parsley at 90 or 50%, [d]seed mix and fresh parsley each at 33 or 45%, [e]seed mix at 70 and fresh parsely at 20%, [f]seed mix at 50 or 90 %; the difference to 100% was grass hay that was available ad litibum with each diet

TA total ash, CP crude protein, CF crude fibre, $NDF_{OM}$ neutral detergent fibre, $ADF_{OM}$ acid detergent fibre (values corrected for residual ash), Na sodium, K potassium, Ca calcium, P phosphorus, Mg magnesium

**Table 1.2.** Food intake and apparent digestibilities measured on the different diets in rabbits in this study

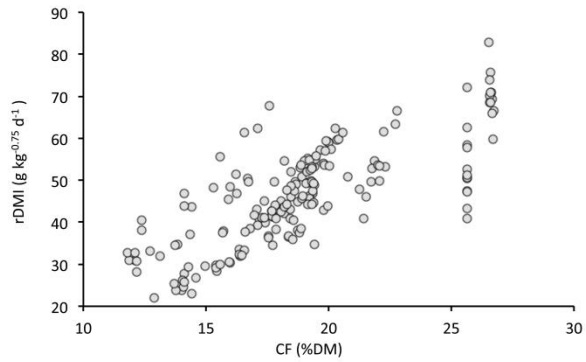
| Diet | Body mass kg | rDMI $g\ kg^{-0.75}\ d^{-1}$ | OM | Na | K | Ca | P | Mg |
|---|---|---|---|---|---|---|---|---|
| | | | % | | | | | |
| Hay100 | 1.4 ±0.4 | 53 ±9 | 45 ±4 | 28 ±53 | 80 ±5 | 50 ±7 | -9 ±23 | -55 ±53 |
| HRP90 | 1.5 ±0.4 | 70 ±6 | 47 ±9 | 76 ±7 | 85 ±4 | 53 ±9 | 5 ±16 | -41 ±68 |
| Pellet90 | 1.7 ±0.4 | 46 ±5 | 62 ±5 | 82 ±5 | 82 ±5 | 34 ±11 | -1 ±14 | -81 ±36 |
| Parsley90 | 1.5 ±0.4 | 51 ±8 | 65 ±9 | 92 ±4 | 91 ±4 | 61 ±7 | 9 ±13 | -29 ±50 |
| Parsley50 | 1.4 ±0.4 | 54 ±7 | 59 ±8 | 86 ±11 | 89 ±4 | 58 ±7 | 6 ±16 | -33 ±38 |
| SeedParsley45 | 1.7 ±0.4 | 38 ±6 | 72 ±5 | 90 ±4 | 90 ±3 | 45 ±11 | -15 ±20 | -74 ±43 |
| SeedParsley33 | 1.5 ±0.4 | 47 ±6 | 66 ±6 | 87 ±7 | 89 ±4 | 57 ±6 | 3 ±15 | -32 ±50 |
| Seed70Parsley20 | 1.6 ±0.4 | 41 ±11 | 70 ±5 | 85 ±8 | 86 ±7 | 48 ±17 | -9 ±31 | -57 ±36 |
| Seed50 | 1.6 ±0.4 | 38 ±11 | 63 ±6 | 82 ±6 | 85 ±4 | 43 ±15 | -18 ±26 | -67 ±52 |
| Seed90 | 1.6 ±0.4 | 43 ±15 | 69 ±7 | 83 ±10 | 79 ±8 | 44 ±22 | -1 ±25 | -56 ±60 |

rDMI relative dry matter intake, OM organic matter, Na sodium, K potassium, Ca calcium, P phosphorus, Mg magnesium

**Table 1.3.** AIC values for models explaining the concentration of digestible mineral in the diet. For each mineral, the simple model with mineral concentration as the only independent variable (without and with accounting for individual as random factor), and the best models of combinations with other mineral concentrations, with diet descriptors, and combinations of mineral concentrations, diet descriptors and fibre concentrations (cf. Table 1.1) are shown.

| Dependent | Model | Random factor | AIC |
|---|---|---|---|
| dNa | Na | - | -941.170 |
| | Na | Individuum | -962.392 |
| | Na + K + P | Individuum | -1012.247 |
| | Na + Hay + Nonforage | Individuum | -1004.956 |
| | Na + K + Hay + NDF + ADF | Individuum | -1015.443 |
| dK | K | - | -282.142 |
| | K | Individuum | -360.621 |
| | K +Ca + Na | Individuum | -393.345 |
| | K +Parsley | Individuum | -391.763 |
| | K +Na + NDF + Parsley | Individuum | 398.852 |
| dCa | Ca | - | -220.630 |
| | Ca | Individuum | -274.813 |
| | Ca + K | Individuum | -288.551 |
| | Ca + Hay + Nonforage | Individuum | -285.587 |
| | Ca + K + ADF | Individuum | -287.017 |
| dP | P | - | -438.284 |
| | P | Individuum | -456.640 |
| | P + K + Na | Individuum | -461.011 |
| | P + Nonforage + Parsley | Individuum | -459.134 |
| | P + Na + Nonforage | Individuum | -461.270 |
| dMg | Mg | - | -581.798 |
| | Mg | Individuum | -593.635 |
| | Mg + K | Individuum | -597.333 |
| | Mg + Parsley | Individuum | -596.086 |
| | Mg + Parsley + NDF | Individuum | -595.929 |

A




B

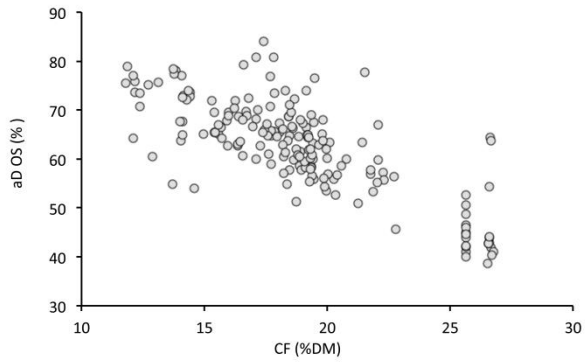



**Figure 1.1.** Relationships of dietary crude fibre (CF; in % dry matter DM) and (A) the relative dry matter intake (rDMI in g per unit metabolic body mass and day) or (B) the apparent digestibility (aD) of organic matter (OM) in the rabbits (*Oryctolagus cuniculus*) of this study; the regression equation [with 95%CI for parameter estimates] was aD OM = 105.2 [99.9; 110.5] – 2.27 [-2.52; -2.01] CF (accounting for individuum as a random factor).

*5.1.2 Literature data*

When compared to literature data, the results of this study generally matched the overall patterns (Fig. 1.2-5), with the exception for the comparatively low Mg digestibilities measured in this study (Fig. 1.4D), a systematic difference in the relationship of dietary CF and aD OM in horses as compared to the smaller animals (Fig. 1.3), and with a deviation of guinea pig digestibility for Na and K as compared to other species (Fig. 1.4AB). When comparing the regression equations for horses and small hindgut fermenters (Table 1.4), there was generally overlap in the 95% confidence intervals of parameter estimates, with some notable exceptions. The slope of the aD OM-CF relationship of horses was lower than, and did not overlap with, rabbits and guinea pigs, with the slope of chinchillas and degus overlapping with both groups (Table 1.4). The slope of the dNa-Na and dK-K relationship of guinea pigs was lower than, and did not overlap with, that of the other species (Table 1.4). The slope of the dCa-Ca relationship in horses was lower than, and did not overlap with, that of rabbits, guinea pigs and degus, whereas there was no significant slope in the chinchilla (Table 1.4). The slope of the dP-P relationship of guinea pigs was higher than, and did not overlap with, that of horses, whereas it overlapped in all other species (Table 1.4). Finally, the slope of the dMg-Mg relationship in horses was lower than, and did not overlap with, that of rabbits and ginea pigs.

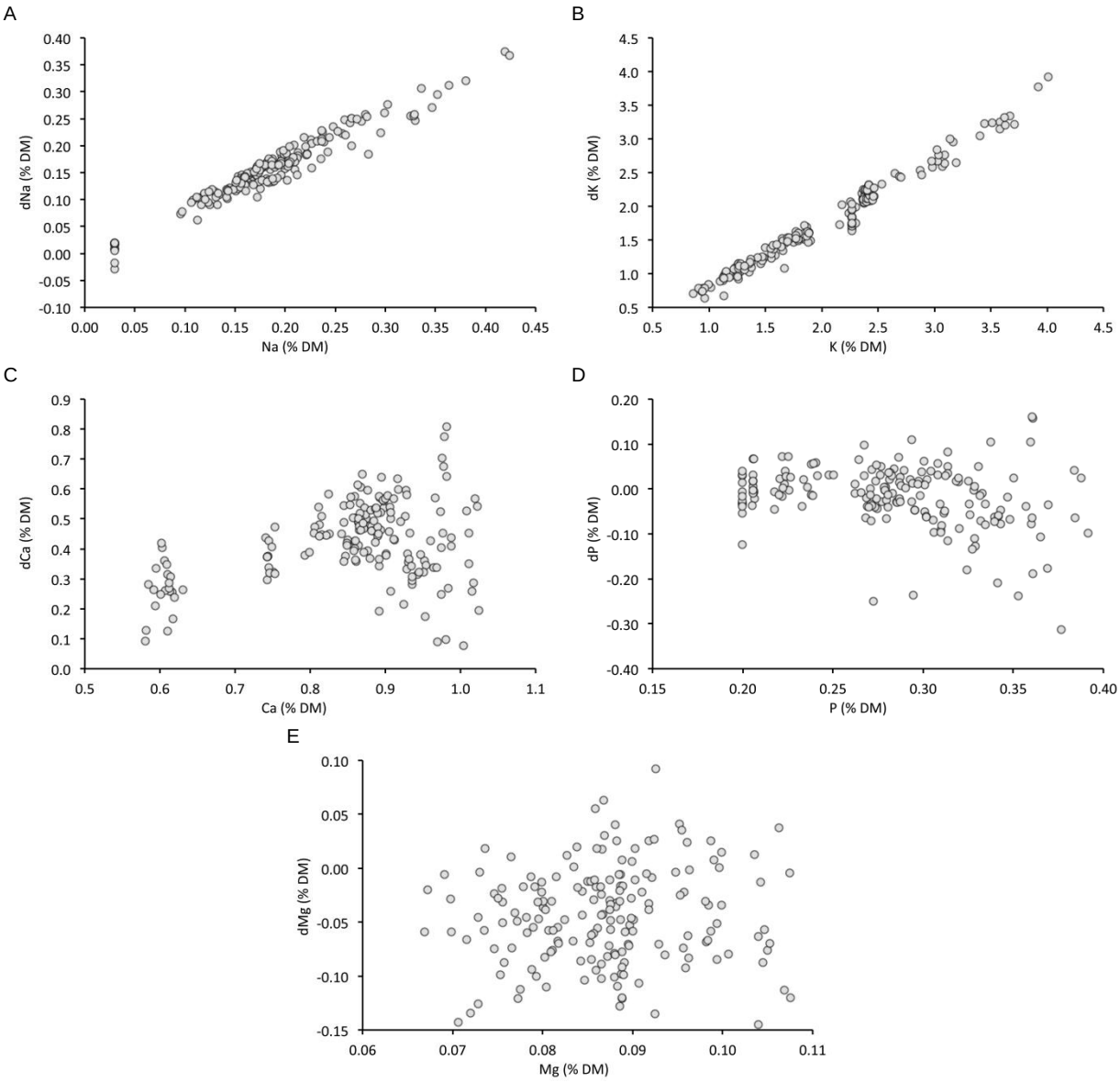



**Figure 1.2.** Relationships between mineral content and digestible (d) mineral content for (A) sodium (Na); regression equation [with 95%CI for parameter estimates] was dNa = 0.009 [0.001; 0.017] + 0.89 [0.86; 0.93] Na, (B) potassium (K), dK = -0.209 [-0.271; -0.147] + 0.973 [0.95; 1.00] K, (C) calcium (Ca), dCa = -0.088 [-0.216; 0.040] + 0.60 [0.46; 0.74] Ca, (D) phosphorus (P), dP = 0.035 [-0.040; 0.111] - 0.18 [-0.44; 0.08] P, (E) magnesium (Mg), dMg = -0.053 [-0.126; 0.020] + 0.11 [-0.72; 0.91] Mg, in the rabbits (*Oryctolagus cuniculus*) of this study. All regression equations calculated accounting for individuum as a random factor.

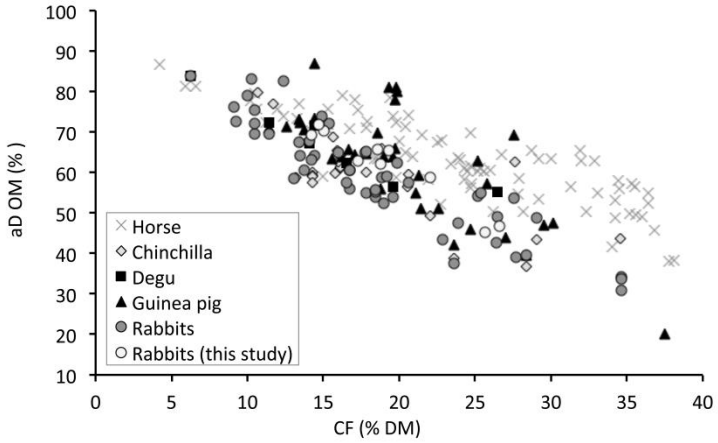



**Figure 1.3.** Relationship of dietary crude fibre (CF; in % dry matter) and the apparent digestibility (aD) of organic matter (OM) in the rabbits (*Oryctolagus cuniculus*) of this study (means of assessed diets) as compared to literature data for rabbits (Slade and Hintz 1969; Fekete and Gippert 1985; De Blas et al. 1986; Sakaguchi et al. 1987; Bucher 1994; Schwabe 1995; Wenger 1997; Schröder 2000; Zumbrock 2002; Clauss et al. 2012; Hommel 2012), guinea pigs (*Cavia porcellus*) (Slade and Hintz 1969; Sakaguchi et al. 1987; Sakaguchi et al. 1992b; Sakaguchi and Ohmura 1992; Schwabe 1995; Meyer et al. 1996b; Wenger 1997), degus (*Octodon degus*) (Sakaguchi and Ohmura 1992; Schröder 2000; Hommel 2012), chinchillas (*Chinchilla laniger*) (Schwabe 1995; Wenger 1997; Schröder 2000; Hansen 2012) and domestic horses (data collection from Kienzle et al. 2002). Note the less steep decrease of aD OM with increasing CF in horses as compared to the other species.

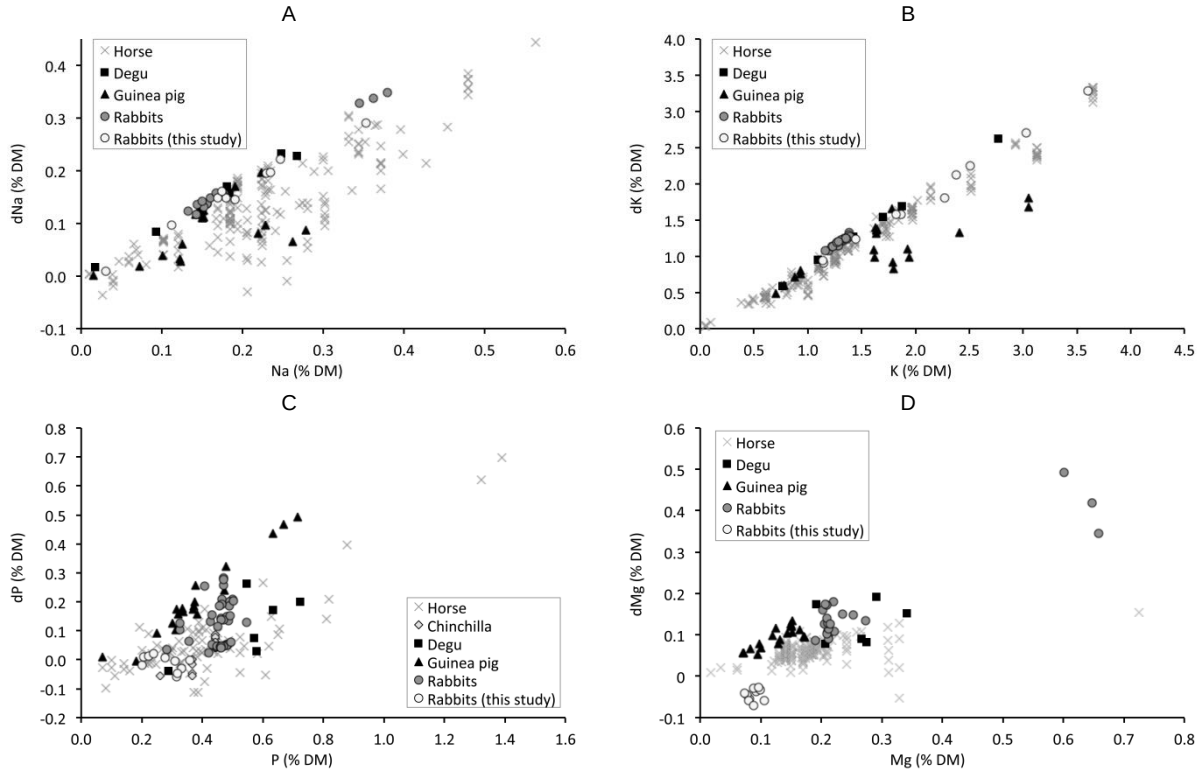



**Figure 1.4.** Relationships between mineral content and digestible (d) mineral content for (A) sodium (Na), (B) potassium (K), (C) phosphorus (P), (D) magnesium (Mg) in the rabbits (*Oryctolagus cuniculus*) of this study (means of assessed diets) as compared to literature data for rabbits (Carstensen 1984; Schröder 1985; Bourdeau et al. 1986; Kamphues et al. 1986; Barr et al. 1991; Clauss et al. 2012; Hommel 2012), guinea pigs (*Cavia porcellus*) (Meyer et al. 1996a; Meyer et al. 1996b), degus (*Octodon degus*) (Hommel 2012), chinchillas (*Chinchilla laniger*) (Hansen 2012) and domestic horses (data collection from Clauss et al. 2007b)

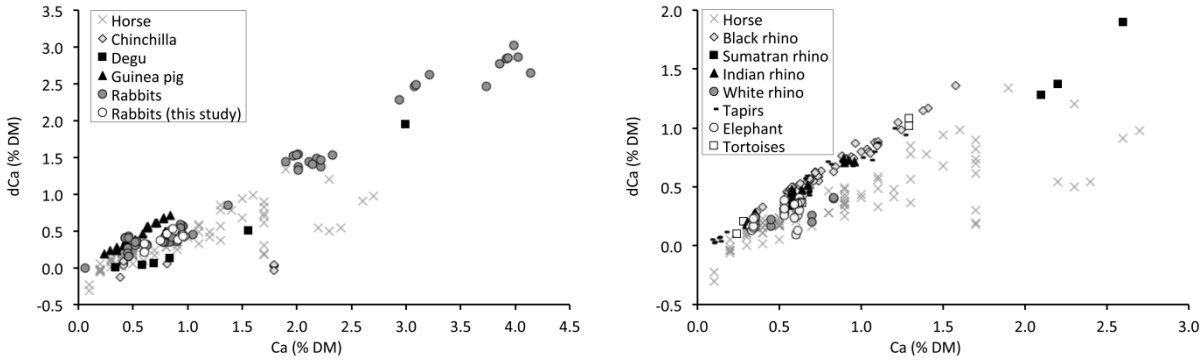



**Figure 1.5.** Relationships between mineral content and digestible (d) mineral content for calcium in (A) the rabbits (*Oryctolagus cuniculus*) of this study (means of assessed diets) and compared to literature data for rabbits (Buss and Bourdeau 1984; Carstensen 1984; Schröder 1985; Bourdeau et al. 1986; Kamphues et al. 1986; Barr et al. 1991; Ritskes-Hoitinga et al. 2004; Clauss et al. 2012; Hommel 2012), guinea pigs (*Cavia porcellus*) , degus (*Octodon degus*) (Hommel 2012), chinchillas (*Chinchilla laniger*) (Hansen 2012), and (B) in black rhinos (*Diceros bicornis*) (Clauss et al. 2007b), Sumatran rhino (*Dicerorhinus sumatrensis*) (Dierenfeld et al. 2000), Indian rhino (*Rhinoceros unicornis*) (Clauss et al. 2005b), white rhino (*Ceratotherium simum*) (Frape et al. 1982), Malayan and lowland tapir (*Tapirus* spp.) (Clauss et al. 2009), Asian elephants (*Elephas maximus*) (Clauss et al. 2003) and tortoises (*Geochelone nigra*, *Testudo hermanni*) (Liesegang et al. 2001; Liesegang et al. 2007) as compared to domestic horses (data collection from Clauss et al. 2007b).

**Table 1.4.** Regression equations (y = a + b x) in various herbivore species

| Species | a | b | a | b | a | b |
|---|---|---|---|---|---|---|
| | aD OM = a + b CF | | dNa = a + b Na | | dK = a + b K | |
| Horse | 88.6 [85.4; 91.8] | -1.06 [-1.18; -0.95] | -0.052 [-0.068; -0.036] | 0.84 [0.78; 0.89] | -0.118 [-0.153; -0.083] | 0.88 [0.86;0.90] |
| Rabbit* | 91.4 [87.2; 95.5] | -1.70 [-1.91; -1.49] | -0.017 [-0.025; -0.010] | 0.98 [0.96; 1.00] | 0.029 [-0.042; 0.099] | 0.88 [0.84; 0.92] |
| Guinea pig | 99.7 [88.3; 111.0] | -1.84 [-2.37; -1.30] | 0.023 [-0.032; 0.078] | 0.42 [0.10; 0.75] | 0.338 [0.056; 0.619] | 0.46 [0.31; 0.62] |
| Chinchilla | 83.4 [74.9; 92.0] | -1.31 [-1.75; -0.87] | - | - | - | - |
| Degu | 90.0 [82.0; 97.9] | -1.48 [-1.96; -1.00] | 0.002 [-0.015; 0.019] | 0.89 [0.80; 0.98] | -0.167 [-0.199; -0.135] | 1.01 [0.99; 1.02] |
| | dCa = a + b Ca | | dP = a + b P | | dMg = a + b Mg | |
| Horse | -0.020 [-0.088; 0.048] | 0.40 [0.34; 0.46] | -0.121 [-0.153; -0.088] | 0.44 [0.37; 0.51] | 0.039 [0.030; 0.049] | 0.12 [0.07; 0.16] |
| Rabbit* | -0.147 [-0.201; -0.092] | 0.76 [0.73; 0.79] | -0.146 [-0.246; -0.047] | 0.58 [0.35; 0.81] | -0.079 [-0.109; -0.048] | 0.84 [0.72; 0.95] |
| Guinea pig | -0.032 [-0.106; 0.043] | 0.87 [0.74; 1.00] | -0.117 [-0.157; -0.078] | 0.85 [0.75; 0.94] | 0.013 [-0.017; 0.043] | 0.63 [0.40; 0.86] |
| Chinchilla | -0.027 [-0.048; 0.102] | -0.01 [-0.07; 0.06] | -0.314 [-0.450; -0.177] | 0.83 [0.49; 1.18] | - | - |
| Degu | -0.428 [-0.649; -0.207] | 0.76 [0.60; 0.91] | -0.176 [-0.501; 0.149] | 0.53 [-0.04; 1.09] | 0.085 [-0.148; 0.318] | 0.16 [-0.71; 1.04] |

data sources indicated in Fig. 3-5; *including diet means of this study
aD apparent digestibility [%], OM organic matter, Na sodium, K potassium, Ca calcium, P phosphorus, Mg magnesium, d digestible mineral
[all in % dry matter]

### *5.2 Digestive physiology of the plains viscacha compared to other hindgut fermenters*

The digestive tract of the plains viscacha is characterised by a simple stomach, a voluminous caecum, a colon ascendens with a colonic furrow whose borders are defined by simple muscular ridges, and a long descending colon (Fig. 2.1). The wet weight of total gut contents represent 11.0 ±3.5 % of body mass (Table 2.1).

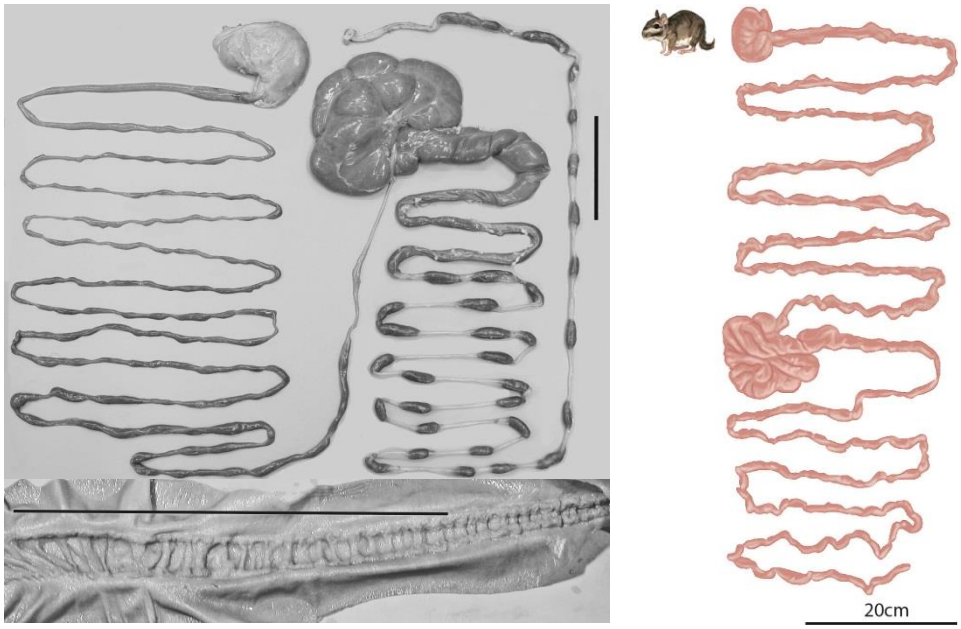



**Figure 2.1.** Macroscopic anatomy of the digestive tract of plains viscacha (*Lagostomus maximus*), with photographic documentation of a complete digestive tract, the colonic furrow on the inside of the cranial part of the colon ascendens, and a schematic graphic representation (drawn by Jeanne Peters). Scale bars on the right indicate 10 cm.

**Table 2.1.** Anatomical measurements of the digestive tract in two male and two female adult plains viscachas (*Lagostomus maximus*)

| | ---------- Male ---------- | | | ---------- Female ---------- | | |
|---|---|---|---|---|---|---|
| Body mass (kg) | 4.5/ 4.3 | | | 2.4/4.0 | | |
| Body length (cm) | 56/53 | | | 43/52 | | |
| | Length (cm) | Empty mass (g) | Wet content mass (g) | Length (cm) | Empty mass (g) | Wet content mass (g) |
| Stomach | 8/11 | -/23 | -/58 | 12/10 | 8/21 | 44/120 |
| Small intestine | 292/381 | -/44 | -/85 | 280/289 | 16/ 44 | 25/ 62 |
| Caecum | 15/15 | -/30 | -/217 | 16/10 | 13/21 | 212/75 |
| Colon ascendens | 28/49 | -/14 | -/43 | 29/27 | 8/19 | 39/38 |
| Rest of colon & rectum | 216/213 | -/94 | -/32 | 217/130 | 15/13 | 36/24 |

There was no pronounced feeding selectivity in the animals in Exp2 (Table 2.2), with ingested hay not differing significantly from the offered hay in terms of crude protein, crude fibre or NDF ($p>0.05$ in all cases). The relative dry matter intake (rDMI) varied, across experiments, from 38 to 51 g $kg^{-0.75}$ $d^{-1}$ (Table 2.3) and was not significantly correlated to dietary fibre measures or organic matter digestibility ($p>0.05$ in all cases). There was no significant difference in rDMI between Exp1A and Exp1B (paired t-test, $p=0.295$). In contrast, rDMI in Exp2A was significantly higher than that of Exp2B or Exp2C, with no difference between the latter two (paired t-test with Sidak adjustment, $p=0.001$, 0.014 and 0.146, respectively). The total water intake (only measured in Exp2) was tightly correlated to DMI ($R=0.86$, $p<0.001$) (Fig. 2.2); total water intake averaged at 1.2 ±0.3 g $gDMI^{-1}$, which is lower than reported for guinea pigs, degus, chinchillas and rabbits on diets consisting of dry feeds (Fig. 2.2). However, the only significant difference was between guinea pigs and all other species (ANOVA and Sidak post hoc tests, $p<0.001$ for comparisons with guinea pigs, $p>0.05$ for all other comparisons).

Particle and solute MRT ranged at 23-31 h (Table 2.3) and were highly correlated with each other ($R=0.93$, $p<0.001$). There was no difference in the MRT of particles and solutes (paired t-test, $p=0.367$), and not significant relationship between body mass, rDMI or relative water intake and a MRT measure ($p>0.05$ in all cases). Behaviour compatible with coprophagy was observed sporadically (Fig. 2.3). The marker excretion patterns showed several secondary peaks suggestive of coprophagy on the grass hay diets (Exp1A, Exp2A) but less so on the pelleted diet (Exp1B) or the lucerne hay diet (Exp3) (Fig. 2.4). Comparing repeated measurements in individuals on two diets, animals had a significantly higher number of secondary marker excretion peaks (median 3, range 2-5) in Exp1A than in Exp1B (median 2, range 1-3) (Wilcoxon signed rank test $p=0.024$).

**Table 2.2.** Nutrient composition (in g per kg dry matter) and gross energy content of feeds and leftovers from three feeding experiments with plains viscachas (*Lagostomus maximus*)

| | Exp1 | | | Exp2 | | | Exp3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | Grass hay | Pellets[1] | Carrots | Grass hay | Hay leftovers | Pellets[2] | Lucerne hay | Hay leftovers | Pellets[3] |
| Total ash | 43 | 84 | 77 | 48 ±6 | 53 ±9 | 104 | 73 ±10 | 100 ±19 | 121 |
| Crude protein | 47 | 255 | 55 | 73 ±5 | 75 ±8 | 147 | 120 ±19 | 149 ±13 | 163 |
| Ether extracts | 10 | 48 | 23 | 14 ±1 | 14 ±3 | 35 | 7 ±0 | 8 ±1 | 16 |
| Crude fibre | 449 | 132 | 92 | 392 ±22 | 397 ±27 | 17 | 469 ±35 | 418 ±62 | 298 |
| NDF | 742 | 223 | 118 | 653 ±22 | 657 ±19 | 323 | 642 ±40 | 568 ±45 | 455 |
| ADF | 438 | 126 | 83 | 352 ±20 | 347±29 | 180 | 515 ±29 | 466 ±55 | 354 |
| ADL | 42 | 17 | 0 | 27 ±7 | 26 ±7 | 38 | 122 ±9 | 106 ±11 | 97 |
| Gross energy (kJ $gDM^{-1}$) | 18.7 | 19.2 | 17.8 | 18.6 ±0.2 | 18.5±0.2 | 17.9 | 18.0 ±0.2 | 17.6 ±0.5 | 17.8 |

[1]commercial guinea pig diet containing grains, soy extraction meal, molasses, grass meal, mineral premix, Meerschweinchen Zucht 3500 (Nafag 9211) Provimi Kliba SA, Kaiseraugst, Switzerland
[2]commercial guinea pig diet containing grains, soy extraction meal, molasses, grass meal, mineral premix, Ergänzungsfutter für Meerschweinchen (Melior 4653) Meliofeed AG, Herzogenbuchsee, Switzerland
[3]pelleted lucerne No. 2805, Provimi Kliba SA, Kaiseraugst, Switzerland

**Table 2.3.** Body mass, food, digestible energy (DE) and water intake, mean retention times of a particle (Cr) and a solute (Co) marker, and nutrient composition of the ingested diet in the different treatments of this study

| | ----- Exp1 (n=7) ----- | | ---------- Exp2 (n=6) ---------- | | | Exp3 (n=3) |
|---|---|---|---|---|---|---|
| | A | B | A | B | C | |
| Body mass (kg) | 3.53 ±1.11 | 3.50 ±0.96 | 3.16 ±0.81 | 3.72 ±1.00 | 3.27 ±0.79 | 4.47 ±1.77 |
| Body mass change (g $d^{-1}$) | -8.7 ±9.3 | 16.3 ±9.8 | -12.7 ±5.7 | -22.1 ±7.7 | -13.2 ±7.5 | nd |
| Dry matter intake (g $kg^{-0.75}$ $d^{-1}$) | 47 ±8 | 50 ±6 | 51 ±9 | 38 ±11 | 43 ±8 | 45 ±11 |
| DE intake (kJ $kg^{-0.75}$ $d^{-1}$) | 307 ±152 | 629 ±83 | 496 ±84 | 446 ±131 | 355 ±69 | 441 ±135 |
| Total water intake (g $kg^{-0.75}$ $d^{-1}$) | nd | nd | 62 ±20 | 39 ±16 | 58 ±18 | nd |
| | | | | | | |
| MRT Cr (h) | 26 ±6 | 30 ±10 | 28 ±5 | | | 24 ±2 |
| MRT Co (h) | 26 ±6 | 31 ±8 | 28 ±3 | | | 23 ±3 |
| | | | | | | |
| Diet composition (g $kgDM^{-1}$) | | | | | | |
| Total ash | 43 | 74 ±2 | 46 ±4 | 85 ±10 | 44 ±3 | 53 ±10 |
| Crude protein | 47 | 192±12 | 66 ±6 | 126 ±10 | 72 ±7 | 100 ±21 |
| Ether extracts | 10 | 38 ±2 | 15 ±4 | 29 ±3 | 15 ±2 | 9 ±3 |
| Crude fibre | 449 | 202 ±21 | 351 ±27 | 246 ±40 | 392 ±26 | 485 ±58 |
| NDF | 742 | 334 ±34 | 604 ±16 | 433 ±35 | 666 ±15 | 676 ±18 |
| ADF | 438 | 194 ±21 | 320 ±14 | 244 ±22 | 364 ±22 | 532 ±48 |
| ADL | 42 | 22 ±2 | 18 ±0 | 38 ±0 | 30 ±0 | 135 ±16 |
| Gross energy (kJ $gDM^{-1}$) | 18.7 | 18.9 ±0 | 18.5 ±0.2 | 18.3 ±0.2 | 18.9 ±0.1 | 18.4 ±0.9 |
| Na | 1.4 | 3.9 ±0.2 | 0.3 ±0 | 6.4 ±1.0 | 0.5 ±0.1 | nd |
| K | 13.8 | 20.5 ±0.6 | 14.8 ±2.4 | 11.3 ±0.3 | 15.2 ±4.0 | nd |
| Ca | 4.7 | 10.1 ±0.5 | 4.7 ±0.7 | 15.8 ±1.8 | 3.7 ±0.9 | nd |
| P | 2.0 | 5.4 ±0.3 | 2.8 ±0.3 | 5.7 ±0.6 | 2.4 ±0.4 | nd |
| Mg | 1.5 | 2.9 ±0.1 | 1.9 ±0.3 | 1.8 ±0.2 | 1.5 ±0.2 | nd |
| Cu (mg $kgDM^{-1}$) | 3.8 | 14.3 ±0.9 | 3.2 ±1.6 | 29.4 ±4.1 | 5.7 ±0.5 | nd |
| Zn (mg $kgDM^{-1}$) | 21.4 | 58.5 ±3.2 | 21.9 ±6.4 | 116.7 ±16.6 | 19.6 ±7.8 | nd |

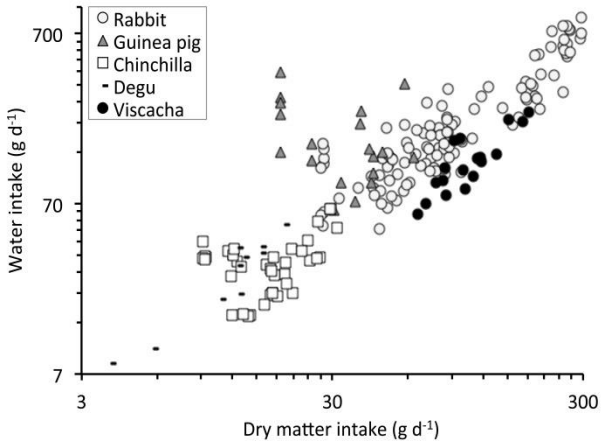



**Figure 2.2.** Total water intake (from diet and drinking water) on diets with only dry components (dry forages, dry commercial feeds) in plains viscachas (*Lagostomus maximus*; mean ±SD ratio of water:dry matter 1.2 ±0.3) of this study, and literature data for rabbits (*Oryctolagus cuniculus*; 2.3 ±0.8), guinea pigs (*Cavia porcellus*; 6.6 ±5.7), degus (*Octodon degus*; 2.3 ±0.5) and chinchillas (*Chinchilla laniger*; 2.0 ±0.9) (Schwabe 1995; Wenger 1997; Schröder 2000; Wolf et al. 2003; Tschudin et al. 2011; Clauss et al. 2012; Hansen 2012; Hommel 2012; Hagen et al. 2014).

**Figure 2.3.** Postural behaviour observed sporadically in plains viscachas (*Lagostomus maximus*) of this study suggestive of coprophagy.

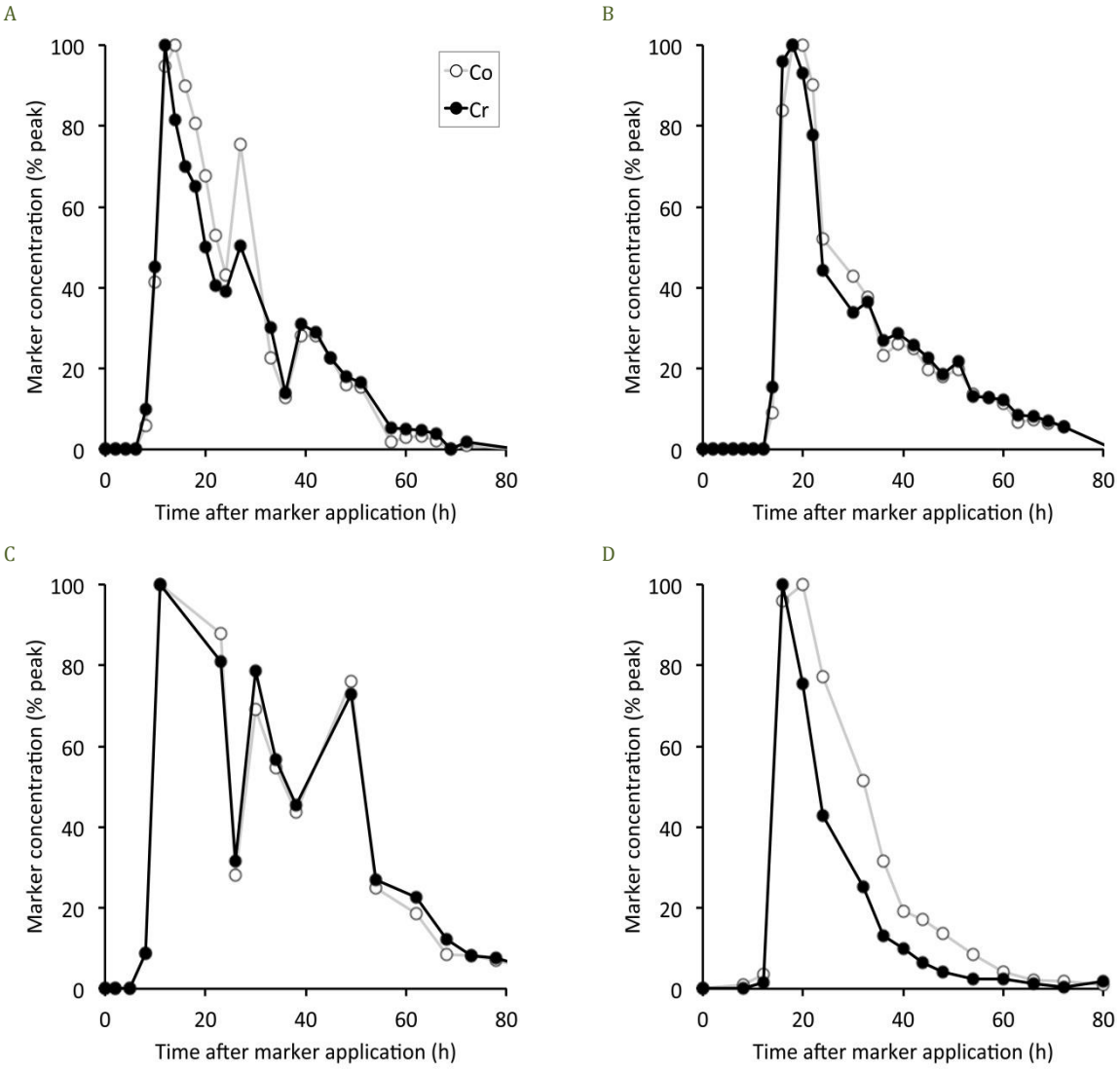



**Figure 2.4.** Excretion patterns for a solute (Co) and a particle (<2mm, Cr) marker in plains viscachas (Lagostomus maximus) in (A) Exp1A – grass hay, (B) Exp1B – a diet of pellets, carrots and grass hay, (C) Exp2A – grass hay, (D) Exp3 – lucerne hay.

There was a significant difference in the relative faecal dry matter excretion between Exp1A and Exp1B (paired t-test, p=0.002), and between Exp2B and Exp2A/C (paired t-test with Sidak adjustment, p<0.001/0.002) but not between the latter two (p=0.802) (Table 2.4). For the two treatments where individual faecal pellet mass was measured, there was a significant difference, with larger faecal pellets on the hay-only diet (Exp2B: 1.82 ±0.61 g; Exp2C: 2.82 ±0.61 g; paired t-test , p<0.001). There was no significant difference in urine excretion between the diet treatments in Exp2 (p always >0.05) (Table 2.4). Urinary glucose as estimated by the Combur test was negative in Exp1A (n=4) but had a median of 30.5 mmol $l^{-1}$ (n=6) in Exp1B, with sample size too low for statistical testing. Similarly, urinary glucose estimated by Combur test were negative in all animals in Exp2A and Exp2C but had a median of 27.8 mmol $l^{-1}$ (n=6) in Exp2B, with the difference between treatments significant at p=0.050 (Friedman's ranked ANOVA). Urinary glucose measured quantitatively in the laboratory had a median (range) of 6.0 (2.9-938.4) mmol $l^{-1}$ for Exp2B and 0.2 (0-0.6) mmol $l^{-1}$ for Exp2C, with a significant difference (Related sample Wilcoxon Rank test, p=0.028).

Serum glucose and fructosamine increased numerically but were not statistically different between Exp1A and Exp1B (6.5 ±1.0 vs. 6.7 ±1.3 mmol $l^{-1}$ and 255 ±24 vs. 281 ±25 µmol $l^{-1}$, respectively; paired t-tests both p>0.05). Serum glucose was 8.5 ±2.1, 9.0 ±4.0 and 7.3 ±1.1 mmol $l^{-1}$, and fructosamine was 333 ±33, 354 ±108 and 300 ±26 µmol $l^{-1}$ in Exp2A, B and C, respectively, with no significant difference between treatments (p>0.05 in all cases).

**Table 2.4.** Faecal excretion, faecal nitrogen, urine output and apparent digestibilities, in the different treatments of this study

| | ----- Exp1 (n=7) ----- | | ---------- Exp2 (n=6) ---------- | | | Exp3 (n=3) |
|---|---|---|---|---|---|---|
| | A | B | A | B | C | |
| Dry matter defecation (g $kg^{-0.75}$ $d^{-1}$) | 28 ±9 | 17 ±4 | 23 ±5 | 13 ±4 | 24 ±5 | 20 ±2 |
| Faecal nitrogen (%DM) | 1.53 ±0.14 | 2.76 ±0.36 | 1.43 ±0.09 | 1.93 ±0.43 | 1.35 ±0.08 | 2.28 ±0.13 |
| Urine excretion (g $kg^{-0.75}$ $d^{-1}$) | nd | nd | 8.5 ±3.5 | 7.2 ±5.9 | 6.2 ±1.7 | nd |
| Apparent digestibilities (%) | | | | | | |
| Dry matter | 45 ±4 | 66 ±7 | 54 ±4 | 65 ±5 | 45 ±4 | 55 ±6 |
| Organic matter | 46 ±4 | 68 ±7 | 55 ±4 | 66 ±5 | 46 ±4 | 57 ±5 |
| Total ash | 24 ±6 | 42 ±8 | 36 ±9 | 54 ±6 | 20 ±11 | 11 ±28 |
| Crude protein | -14 ±14 | 70 ±4 | 38 ±6 | 66 ±9 | 34 ±9 | 26 ±16 |
| Ether extracts | -30 ±16 | 75 ±6 | 34 ±13 | 72 ±6 | 24 ±15 | -23 ±104 |
| Crude fibre | 45 ±7 | 40 ±14 | 41 ±7 | 47 ±11 | 39 ±5 | 56 ±4 |
| NDFom | 44 ±5 | 40 ±14 | 45 ±5 | 50 ±7 | 39 ±4 | 55 ±5 |
| ADFom | 47 ±5 | 39 ±13 | 42 ±7 | 50 ±8 | 36 ±7 | 56 ±2 |
| Gross energy | 42 ±4 | 66 ±7 | 53 ±4 | 65 ±5 | 44 ±4 | 53 ±5 |
| Na | 59 ±4 | 81 ±5 | 4 ±25 | 93 ±1 | 55 ±8 | nd |
| K | 64 ±11 | 88 ±3 | 85 ±5 | 91 ±3 | 76 ±7 | nd |
| Ca | -12 ±16 | 2 ±14 | 6 ±11 | 35 ±10 | -76 ±55 | nd |
| P | -7 ±12 | 1 ±15 | 40 ±12 | 19 ±14 | 0 ±23 | nd |
| Mg | 35 ±6 | 45 ±7 | 52 ±6 | 51 ±5 | 50 ±16 | nd |
| Cu | -23 ±12 | 3 ±13 | -99 ±141 | 55 ±6 | 49 ±17 | nd |
| Zn | -12 ±10 | 4 ±14 | -33 ±44 | 8 ±18 | -146 ±174 | nd |

There was a significant negative relationship between dietary crude fibre and the apparent digestibility of organic matter in the viscachas that was different from the relationship of these measures in rabbits and guinea pigs but similar to that in horses (Fig. 2.5), with a difference in the slope of the relationship (Table 2.5). In contrast, the relationship of nutrient content and digestible nutrient content in the diet did not differ markedly between species for crude protein ether extracts (Fig. 2.6), or for minerals (Fig. 2.7). Confidence intervals for parameter estimates from the corresponding regression equations showed a large degree of overlap (Table 2.5). Faecal nitrogen ranged from 1.1 to 3.0 %DM (mean 1.9 ±0.6) (Table 4) and was positivly correlated with the apparent digestibility of organic matter ($R=0.71$, $p<0.001$).

Although the three viscachas of Exp3 consumed food in the respiration chambers, the respiration quotient was comparatively low (Table 2.6). The mean resting metabolic rate was at 229 ±31 kJ $kg^{-0.75}$ $d^{-1}$, and methane production averaged at 2.01 ±0.64 L $d^{-1}$ or 3.4 ±1.3 % of gross energy intake (Table 2.6). Plotting digestible energy intake (DEI) versus daily body mass changes resulted in a maintenance DEI requirement of 445 kJ $kg^{-0.75}$ $d^{-1}$ in Exp1; when adding the data from Exp2, the requirement changed to 564 kJ $kg^{-0.75}$ $d^{-1}$ (Fig.2.8).

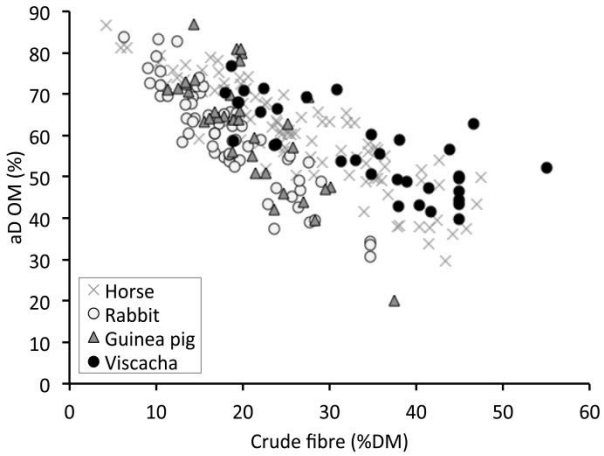



**Figure 2.5.** Relationship of dietary crude fibre and the apparent digestibility (aD) of organic matter (OM) in plains viscachas (*Lagostomus maximus*) of this study, and literature data for horses (*Equus caballus*), rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) (for data sources see Fig. 1.3).

**Table 2.5.** Parameter estimates (with 95% confidence intervals) for regression equations according to y = a + bx (indicated as y-x) in various herbivore species from this study and the literature (for data sources see Fig. 1.4 and 1.5)

| | | aDOM-CF | dCP-CP | dEE-EE | dNa-Na | dK-K | dCa-Ca | dP-P | dMg-Mg | dCu-Cu | dZn-Zn |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Viscacha** | a | 82.1 [74.2;89.9] | -43.7 [-53.7;-33.7] | -12.3 [-1.4;-1.1] | -0.035 [-0.045;-0.025] | -0.222 [-0.466;0.022] | -0.418 [-0.584;-0.252] | -0.002 [-0.072;0.068] | 0.002 [-0.022;0.025] | -0.374 [-0.550;-0.197] | -1.171 [-1.883;-0.459] |
| | b | -0.75 [-0.97;-0.53] | 0.93 [0.84;1.01] | 1.09 [1.02;1.16] | 0.95 [0.92;0.98] | 0.96 [0.80;1.11] | 0.54 [0.36;0.72] | 0.12 [-0.06;0.29] | 0.46 [0.34;0.57] | 0.61 [0.49;0.72] | 0.18 [0.06;0.30] |
| **Rabbit** | a | 91.4 [87.2; 95.5] | -25.4 [-43.7;-7.2] | -6.8 [-12.2;-1.4] | -0.017 [-0.025;-0.010] | 0.029 [-0.042; 0.099] | -0.147 [-0.201;-0.092] | -0.146 [-0.246;-0.047] | -0.079 [-0.109;-0.048] | nd | nd |
| | b | -1.70 [-1.91; -1.49] | 0.86 [0.75;0.97] | 0.86 [0.71;1.02] | 0.98 [0.96;1.00] | 0.88 [0.84;0.92] | 0.76 [0.73;0.79] | 0.58 [0.35;0.81] | 0.84 [0.72;0.95] | nd | nd |
| **Guinea pig** | a | 99.7 [88.3; 111.0] | -37.9 [-58.2;-17.8] | -7.0 [-10.0;-3.9] | 0.023 [-0.032; 0.078] | 0.338 [0.056; 0.619] | -0.032 [-0.106; 0.043] | -0.117 [-0.157; -0.078] | 0.013 [-0.017; 0.043] | nd | nd |
| | b | -1.84 [-2.37; -1.30] | 0.89 [0.76;1.02] | 0.88 [0.80;0.97] | 0.42 [0.10; 0.75] | 0.46 [0.31; 0.62] | 0.87 [0.74; 1.00] | 0.85 [0.75; 0.94] | 0.63 [0.40; 0.86] | nd | nd |
| **Degu** | a | 90.0 [82.0; 97.9] | -43.7 [-53.7;-33.7] | -7.7 [-13.1;-2.3] | 0.002 [-0.015; 0.019] | -0.167 [-0.199; -0.135] | -0.428 [-0.649; -0.207] | -0.176 [-0.501; 0.149] | 0.085 [-0.148; 0.318] | nd | nd |
| | b | -1.48 [-1.96; -1.00] | 0.93 [0.84;1.01] | 0.99 [0.86;1.11] | 0.89 [0.80; 0.98] | 1.01 [0.99; 1.02] | 0.76 [0.60; 0.91] | 0.53 [-0.04; 1.09] | 0.16 [-0.71; 1.04] | nd | nd |
| **Chinchilla** | a | 83.4 [74.9; 92.0] | -60.9 [-90.5;-31.4] | -5.2 [-18.9;8.5] | nd | nd | -0.027 [-0.048; 0.102] | -0.314 [-0.450; -0.177] | nd | nd | nd |
| | b | -1.31 [-1.75; -0.87] | 1.02 [0.84;1.19] | 0.86 [0.30;1.42] | nd | nd | -0.01 [-0.07; 0.06] | 0.83 [0.49; 1.18] | nd | nd | nd |
| **Horse** | a | 88.6 [85.4; 91.8] | -21.7 [-30.2;-13.1] | -1.5 [-4.9;1.9] | -0.052 [-0.068; -0.036] | -0.118 [-0.153; -0.083] | -0.020 [-0.088; 0.048] | -0.121 [-0.153; -0.088] | 0.039 [0.030; 0.049] | -0.033 [-0.368;0.302] | -0.735 [-3.475;2.005] |
| | b | -1.06 [-1.18; -0.95] | 0.85 [0.78;0.93] | 0.46 [0.36;0.55] | 0.84 [0.78; 0.89] | 0.88 [0.86;0.90] | 0.40 [0.34; 0.46] | 0.44 [0.37; 0.51] | 0.12 [0.07; 0.16] | 0.33 [0.18;0.48] | 0.00 [-0.38;0.38] |

aDOM apparent digestibility of organic matter (%), CF crude fibre (in %DM), CP crude protein and EE ether extracts (in g $kgDM^{-1}$), Na sodium, K potassium, Ca calcium, P phosphorus, Mg magensium (in %DM), Cu copper, Zn zinc (in mg $gDM^{-1}$), d indicates the 'apparently digestible' mineral

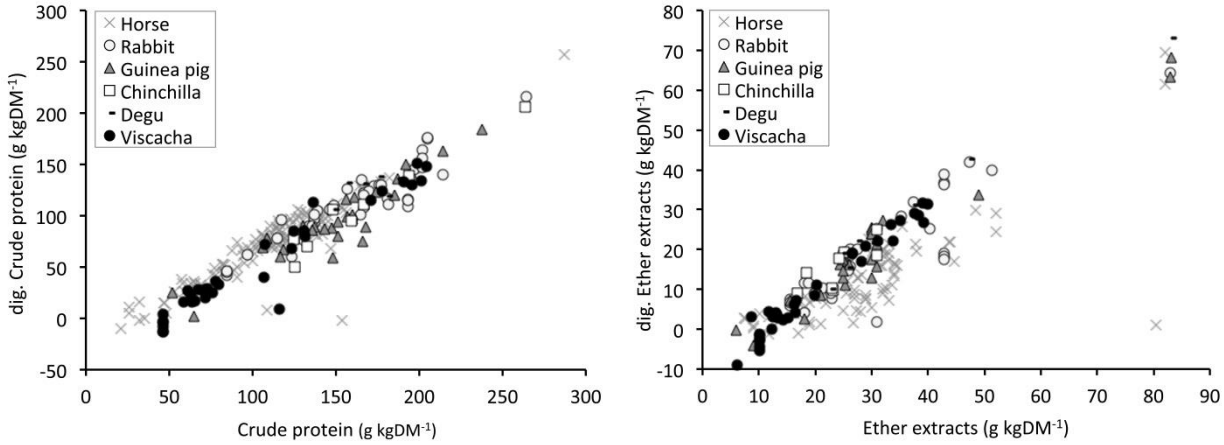



**Figure 2.6.** Relationship of dietary nutrient content (protein or fat) and the digestible nutrient content in plains viscachas (*Lagostomus maximus*) of this study, and literature data for horses (*Equus caballus*), rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) (Slade and Hintz 1969; Sakaguchi et al. 1987; Sakaguchi and Hume 1990; Sakaguchi et al. 1992a; Sakaguchi and Nabata 1992; Sakaguchi et al. 1992b; Sakaguchi and Ohmura 1992; Schwabe 1995; Meyer et al. 1996b; Wenger 1997; Zeyner and Kienzle 2002; Zumbrock 2002; Clauss et al. 2012; Hommel 2012).

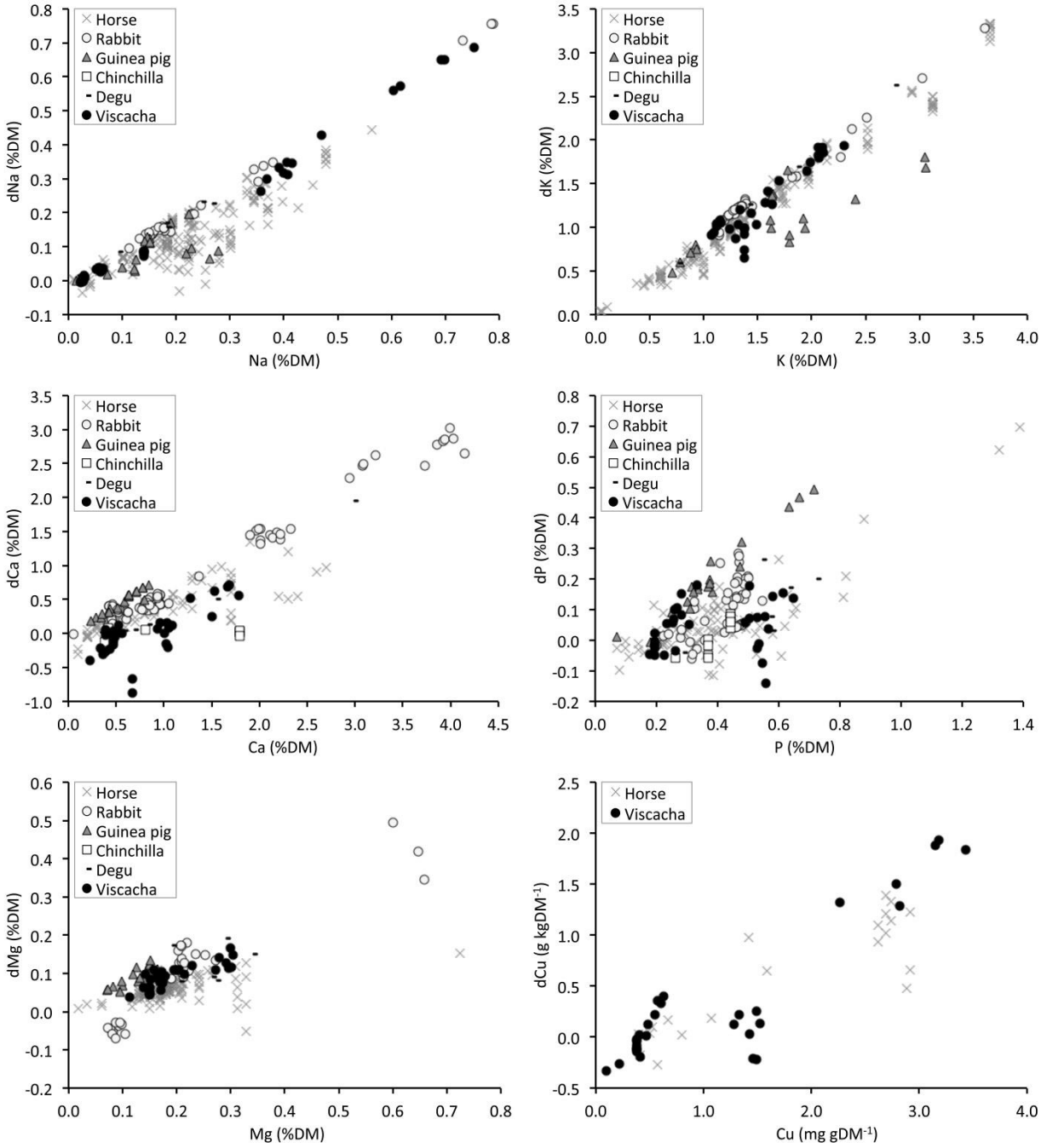



**Figure 2.7.** Relationship of dietary mineral content (sodium, potassium, calcium, phosphorus, magnesum, copper) and the digestible mineral content in plains viscachas (*Lagostomus maximus*) of this study, and literature data for horses (*Equus caballus*), rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) (for data sources see Fig. 1.4 and 1.5).

**Table 2.6.** Consumption of $O_2$ and excretion of $CO_2$ and $CH_4$ in individual plains viscachas (*Lagostomus maximus*) in Exp3 of the present study.

| Individual | | 1 | 2 | 3 |
|---|---|---|---|---|
| $O_2$ | L $day^{-1}$ | 33.9 | 50.5 | 47.4 |
| Metabolic rate | (kJ $kg^{-0.75}day^{-1}$) | 313 | 342 | 238 |
| Resting metabolic rate | (kJ $kg^{-0.75}day^{-1}$) | 244 | 250 | 194 |
| $CO_2$ | L $day^{-1}$ | 27.8 | 39.1 | 36.1 |
| Respiratory quotient* | | 0.82 | 0.77 | 0.76 |
| Methane | L $day^{-1}$ | 1.61 | 2.74 | 1.67 |
| | L $day^{-1}$ $kg^{-1}$ body mass | 0.57 | 0.64 | 0.26 |
| | L $kg^{-1}$ dry matter intake | 13.0 | 21.9 | 11.7 |
| | % of gross energy intake | 2.89 | 4.90 | 2.40 |
| | % of digestible energy intake | 4.95 | 9.74 | 4.75 |
| | L $kg^{-1}$ intake of digestible neutral detergent fibre | 31.7 | 57.1 | 36.2 |

*Calculated as $CO_2/O_2$

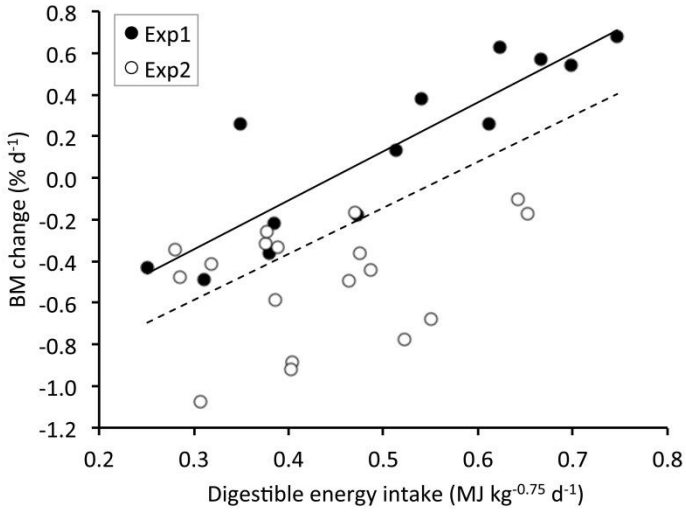



**Figure 2.8.** Relationship between the daily digestible energy intake and body mass changes for the estimation of maintenance energy requirements in plains viscachas (*Lagostomus maximus*) from two experiments at different ambient temperatures (Exp1: 20-22°C; Exp2: 5-10°C). Straight line – regression for Exp1; interrupted line – regression for both experiments combined.

# 6 Discussion

## *6.1 Organic matter and macromineral digestibility of domestic rabbits compared to other hindgut fermenters*

### *6.1.1 General*

The results of this study expand the existing data pool for organic matter and macromineral digestibility in rabbits, indicate a large degree of similarity in digestive processes in hindgut fermenting herbivores, and highlight constraints of comparative datasets. They also support the common knowledge in animal nutrition that the absorption of a nutrient or mineral is influenced by a large variety of factors, whose identification is often beyond the possibility of individual studies or collated datasets, and whose relevance for practical nutritional decisions may often be limited. The results additionally indicate that individual differences have a relevant effect on digestive processes.

There was an evident discrepancy between the visual fit of the data generated in the present study itself and literature data, and the differences in the respective regression equations. Even though data from the rabbits of the present study fitted the overall pattern of the aD OM-CF relationship (Fig. 1.3), the dNa-Na relationship (Fig. 1.4A), or even the dCa-Ca relationship (Fig. 1.5A) in rabbits visually, the 95% confidence intervals for the slope of the regression equations for our own data (given in Fig. 1.1B and 1.2) did not overlap with those based on the larger collection of rabbit data (given in Table 1.4) in the first two examples, and only barely in the latter. Rather than assuming a biological relevance in this discrepancy, it may be more reasonable to interpret such differences mainly as the consequence of differences in data range, methodological differences between studies, and natural variation. Given the influence of individuals documented in the present study (Table 1.3), collating data from different studies (and hence, different individuals) with different ranges of the independent variable can be expected to cause such discrepancies. Therefore, the results of this study support the intuitive concept that only some crude – and therefore potentially more relevant – differences between species will be evident in large, collated datasets, whereas more detailed differences are lost in the data scatter. In particular, the absence of a detectable species difference, such as in the aD OM-CF relationship between rabbits and guinea pigs (Table 1.4), should not lead to the conclusion that these species are really similar in terms of their digestive physiology (as contradicted by several studies cited in the Introduction), but that the difference between them is of a finer magnitude than, e.g., that between these two species and horses. Similarly, the categorisation of chinchillas or degus in

this respect should not be considered exhaustively investigated as long as the range of high-fibre diets used in horses, guinea pigs and rabbits has not been used in these species.

*6.1.2 Dietary fibre and digestibility*

Although the use of crude fibre for the characterisation of herbivore diets has been questioned because, in contrast to the detergent fibre system, the actual nature of the analysed components is relatively undefined (Van Soest 1994), it is considered an attractive measure due to its close correlation with measures of digestibility also documented in the present study; its relationship with organic matter digestibility has traditionally been used to describe species differences in the capacity to deal with plant fibre (Clauss et al. 2006; Kamphues et al. 2014). The other measure most commonly used for such comparisons is neutral detergent fibre (NDF) (Van Soest et al. 1991) which has been used to compare digestive efficiencies of different herbivore species (Clauss et al. 2006).

When assessing species differences from such relationships, it is important to realize that low-fibre diets are usually equally digestible by most species. Therefore, in the low-fibre range, a large degree of data overlap between the species is expected as evident in Fig. 1.3, where no difference between horses and smaller herbivores is evident in the range of 0-10% crude fibre in dietary dry matter. Consequently, the intercept of the aD OM-CF relationship overlaps between the different species (Table 1.4). Species differences in this relationship are evident in the slope, with some species more susceptible to a depression of aD OM due to an increase in dietary fibre than others. Such differences in slope have been proposed for various combinations of the small herbivores included in our data collection (Schwabe 1995; Wenger 1997; Hommel 2012), or for a difference between different rhinoceros species (Clauss et al. 2006). One intuitive interpretation of the pattern observed between horses, rabbits and guinea pigs in Fig. 3 could be that a larger body size (as in the horse) is more suitable for the digestion of a fibrous diet – a viewpoint with a long-standing history in comparative digestive physiology (Demment and Van Soest 1985; Illius and Gordon 1992; but see Clauss et al. 2013; Müller et al. 2013). However, the mentioned differences between individual small hindgut fermenter species or different rhinoceros species, or differences between horses, elephants and rhinoceros (Clauss et al. 2005a), as well as broader species comparisons with a large body mass range (Müller et al. 2013; Steuer et al. 2014), contradict a simplistic link between body mass and digestive efficiency, and indicate that species-specific adaptations may be more important than body mass itself. Notably, there may be other reasons than putative body size-related factors that allowed many smaller species to abandon, over

evolutionary time, a particularly high fibre digestion efficiency (Clauss et al. 2013). The physiological factors that determine species-specific differences in digestive efficiency remain to be identified in most cases. Whether herbivorous rodents are generally similar in the influence of fibre on digestibility, or whether species differences can be demonstrated, remains to be conclusively investigated.

*6.1.3 Macromineral absorption*

Considering the effect that the inclusion of individual as a random factor had on the data fit in the assessed models (reflected in the AIC values, Table 1.3), it is evident that individual differences in absorption between individuals exists. Additionally, the results of the AIC analyses support conclusions made repeatedly in the literature, for example based on simple regressions in horses (Meyer 1980) and guinea pigs (Meyer et al. 1996a), namely that the content of a mineral can influence the absorption of another mineral. That additional factors, such as diet ingredients (the proportion of roughage, nonforage components or parsley in the overall diet) and dietary fibre can influence the absorption of minerals from the gut, matches various findings in horses. Fresh or preserved roughage, or concentrates, have different effects on mineral absorption and ultimately urinary acid-base balance (Kienzle et al. 2006; Goren et al. 2014). Similarly, roughage- or concentrate diets have different effects on the absorption of Ca and Mg (Stadermann et al. 1992). The results of the AIC comparisons offer the hypothesis that variation in K either is a direct influence factor, or represents an important proxy for such a factor, for the observed differences in the absorption of other minerals; K was a component of all best-supported models for the absorption of other minerals (Table 1.3). Should such effects be considered important for animal nutrition, more detailed studies comparing macromineral absorption on roughage and non-roughage diets with carefully balanced mineral concentrations would be required.

The tight relationship between mineral and digestible mineral content for Na and K, with slopes (indicating the 'true' digestibility) close to 1 corroborate the concept that these minerals are generally absorbed nearly completely, and that there is little difference between herbivore species (Robbins 1993). The major difference described between herbivore species in this respect is a generally higher level of endogenous Na losses (represented by the intercept of the dNa-Na relationship) in black rhinoceros (*Diceros bicornis*) as compared to the domestic horse (Clauss et al. 2007b) and, given the data collected in Fig. 1.4A, also as compared to rodents and rabbits. It appears questionable whether the finding that guinea pigs

deviate from the general pattern with a lower slope for both minerals (Table 1.4) is representative of a species peculiarity or a peculiarity of the respective study.

A putative ultimate explanation for the rabbit's strategy of absorbing the majority of dietary Ca from the gut and excreting surplus via urine is that this route of elimination prevents a recycling of Ca via coprophagy (Kamphues et al. 1986). While this explanation is compatible with the presence of this strategy in fossorial and non-fossorial rodent species (Shirley and Schmidt-Nielsen 1967; Kaufman et al. 1976; Haim et al. 1985b; Buffenstein and Yahav 1991; Skinner et al. 1991; Haim et al. 1992; Pitcher et al. 1992; Shore et al. 1992; Pitcher and Buffenstein 1994), it cannot explain why hindgut fermenters not practicing coprophagy have a similar Ca metabolism, such as wild equids, tapirs, rhinoceroses, elephants (Hintz et al. 1976; Schryver et al. 1983; Clauss et al. 2003; Clauss et al. 2005b; Clauss et al. 2007b; Clauss et al. 2009), hyraxes (Leon and Belonje 1979) and also herbivorous tortoises (Liesegang et al. 2001; Liesegang et al. 2007) (Fig. 1.5B). Similarly, the hypothesis that urinary Ca-bicarbonate elimination represents an adaptation of fossorial animals to their hypercapnic environment (Haim et al. 1985a; Haim et al. 1987) cannot explain this mechanism in animals not constrained by the $CO_2$ levels of their environment. An alternative explanation for the peculiar Ca metabolism is that because in plants, a high proportion of Ca is bound to cell walls, hindgut fermenters, which digest cell walls only in the hindgut (in contrast to foregut fermenters that 'release' the Ca prior to the small intestine), had to evolve particularly efficient Ca absorption mechanisms (Pitcher and Buffenstein 1994). However, this approach neither matches the observation that Ca absorption is higher, not lower, in horses fed roughage (with potentially less available Ca) as compared to (mineralized) concentrate diets (with potentially more available Ca) of similar Ca content (Stadermann et al. 1992), nor the finding that some hindgut fermenters with natural diets particularly high in Ca have particularly high Ca absorption efficiencies (Clauss et al. 2007b; Clauss et al. 2009). Thus a potential explanation might be that hindgut fermenters eliminate Ca via urine to maintain levels of available P in the digesta that is required by gut microbes (Clauss et al. 2007b).

Whatever the underlying pattern, chinchillas appear to be outliers to this pattern (Fig. 1.5A, Table 1.4), which has been interpreted as an adaptation to reduce urinary water losses (Hagen et al. 2014). Nevertheless, an increase of urinary Ca concentration with putatively increasing dietary Ca intake, in spite of an increase in urinary volume (as the diet richer in Ca also contained more water), has also been observed in chinchillas (Kohl 1980), and urinary Ca levels were not evidently different between chinchillas and several other rodents, including

guinea pigs (Bellamy and Weir 1972). A particular challenge in determining Ca digestibility in many small rodents might be that Ca concentrations measured in faeces could be influenced by urine often deposited on the faeces. Therefore, further investigations on Ca in chinchillas and other aridity-adapted rodents, including diets with higher Ca levels, could be particularly revealing. This would also be interesting given the finding that in terms of P digestibility, chinchillas do not differ from rabbits and the other rodents (Table 1.4). The fact that rabbits and rodents display a numerically higher 'true' P digestibility than horses (Table 1.4), whereas black rhinoceros and tapirs are similar to horses (Clauss et al. 2007b; Clauss et al. 2009), could suggest that the process of coprophagy recycles, amongst other nutrients, microbial P and thus leads to a reduced excretion in the faeces.

The absorption mechanisms for Mg have been shown to be similar to those of Ca in different species (Hintz and Schryver 1973; Reinhardt et al. 1988; Stadermann et al. 1992), and similarities in the dMg-Mg relationship to the dCa-Ca relationship, as evident from Fig. 1.4D and 1.5A, have also been described in other species (Clauss et al. 2007b; Clauss et al. 2009). The generally low Mg digestibilities in the present study, however, remain unexplained; they are out of line with other results from rabbits and other animals (Fig. 1.4D). To conclude, data from experiments with a large variety of diets allow comparisons among species even if derived from different studies, although variation between study methods may blur detailed differences. Further collation of such data bears the potential to corroborate the homology of digestive processes in a large variety of species, and to detect outliers with partiular adaptations.

### *6.2 Digestive physiology of the plains viscacha compared to other hindgut fermenters*

#### *6.2.1 General*

The results of this study characterise and confirm the plains viscacha as a typical herbivorous rodent with a comparatively high digestive efficiency, a mucus-trap colonic separation mechanism, a digestive strategy that includes a flexible degree of coprophagy, a calcium metabolism like many other herbivorous hindgut fermenters, a low metabolic rate, and a susceptibility for diet-induced diabetes.

#### *6.2.2 Limitations of this study*

A common challenge in digestion experiments with rodents is the potential contamination of faeces with urine, even when animals are kept in metabolism cages. This may not be noticed at the time the faeces are collected because the urine mave have already dripped off the faecal

pellets, with urinary components nevertheless contaminating the faecal sample – and hence leading to lower apparent digestibility measures for the respective nutrients. Two seeming outliers that have particularly low apparent digestibilities for protein (but notably not for lipids that are not excreted via urine, Fig. 2.6), potassium, calcium and phosphorus (Fig. 2.7) might represent such cases. Thus, the habit of many rodents to deposit urine directly on their own faeces may render digestibility measurements, especially those of minerals, problematic.

Selective feeding behaviour can play an important role in the digestive strategy of rodents (Justice and Smith 1992). For example, differences in the degree of feeding selectivity could be demonstrated between rabbits and guinea pigs (Franz et al. 2011a). However, the experimental setup and the diet used will influence possible measurements. The body size of the plains viscachas makes a selective feeding on pelleted diets unlikely; this has been reported for smaller rodents (Justice and Smith 1992; Cameron and Speakman 2010). In contrast, the feeding of dried forages might represent challenges. For example, the lower crude protein and higher fibre levels of the ingested alfalfa hay as compared to the offered one in Exp3 (Table 2.2) are best explained by crumbling losses of leafy components. On the one hand, the lack of evident feeding selectivity in Exp2 and Exp3 suggests that the results of Exp1 are not unduly compromised by the lack of nutrient analyses of leftovers, and is in line with observations that plains viscachas apparently do not selectively target the most easily digestible plants in their natural habitats (Branch et al. 1994). On the other hand, it might be interesting to investigate whether different ways of '*ad libitum*' feeding can influence results on feeding selectivity; ad libitum feeding is achieved by ensuring that there are always leftovers the next time a diet item is replaced. Yet, for practical reasons, feeding is usually organised in such a way that these leftovers are of a limited amount, and hence typically do not exceed the amount consumed by the animals. Offering diets in much greater abundance, i.e. where leftovers exceed the amount consumed in different degrees of magnitude, might result in different selection opportunities and therefore have an influence on measures of feeding selectivity that has not been tested to date.

Another limitation is the collation of data from different individual experiments. In this study, conditions in Exp2 were different both in terms of ambient temperature and the holding facilities. According to the results of Kohl (1980), the animals of Exp2 were challenged in their temperature regulation, which might have contributed to generally higher weight losses at similar DE intakes (Fig. 1.8). Additionally, housing conditions of Exp2, in which the collection period did not take place in the familiar surroundings, but in modified metabolism cages, might have led to a higher stress level that also contributed to higher weight losses at

similar DE intakes. Generally, plains viscachas are known to be more easily agitated than many other, smaller rodents (Weir 1970; Kohl 1980). One possible reason for this might be body size; smaller species might more easily feel protected in the shelters provided in experimental settings. In contrast, to feel protected from human handlers, viscachas might have to be provided with burrows of a scale that makes experimental measurements impossible.

*6.2.3 Adaptations to aridity and fossoriality*

Several measures in plains viscachas suggest a particular adaptation to arid environments, even if the species is represented in biomes of different humidity (Jackson et al. 1996). The family Chinchillidae, to which the plains viscacha belongs together with the chinchillas (*Chinchilla* spp.) and the mountain viscachas (*Lagidium* spp.) is characterised by a particularly long colon (Gorgas 1966), which indicates a high capacity for water reabsorption from digesta at this stie. The measurements of the digestive tract sections of the present study match those reported by Gorgas (1966). The comparatively low water intake in the plains viscachas of Exp2 might also indicate comparatively low water requirements, as also suggested for chinchillas (Hagen et al. 2014). The Chinchillidae are additionally characterised by the ability to produce highly concentrated urine (Weisser et al. 1970; Kohl 1980), and by low metabolic rates (Kohl 1980; Arends and McNab 2001; Cortés et al. 2003; Tirado et al. 2007).

At 229 kJ $kg^{-0.75}$ $d^{-1}$, the resting metabolism of the three plains viscachas of Exp3 was below the mammalian average basal metabolic rate of 293 kJ $kg^{-0.75}$ $d^{-1}$ (Kleiber 1961), but very similar to the resting metabolic rate measured in two plains viscachas by Kohl (1980) of 216 kJ $kg^{-0.75}$ $d^{-1}$. A generally low metabolism in fossorial mammals is usually explained as an adaptation to prevent hypercapnic conditions in the burrow system (McNab 1966; McNab 1979). Additionally, the strategy to absorb a large proportion of Ca from the gut (see Fig. 1.5) and excrete Ca as bound to carbonate via urine should be advantageous for fossorial animals, as it allows the excretion of $CO_2$ without increasing the hypercapnic load of the environment (Haim et al. 1985a; Haim et al. 1987). The fact that some of the excreted $CO_2$ was not exhaled but bound in urine could partly explain the low respiration quotients measured in this study (Table 2.6) even though animals consumed food in the respiration chambers. The low metabolic rate of the species is also evident in the low DE requirements identified in Exp1 (Fig. 2.8) of 445 kJ $kg^{-0.75}$ $d^{-1}$, which are at the lower end of the average range estimated for mammalian hindgut fermenters of 440-660 kJ $kg^{-0.75}$ $d^{-1}$ (Clauss et al. 2005b).

*6.2.4 Colonic separation mechanism and coprophagy*

As in other hystricomorph rodents, which all have a colonic furrow (Gorgas 1966), and also in muroid rodents, there is no difference in the mean retention time of solute and particle markers in plains viscachas, corroborating that, in contrast to the colonic separation mechanism of rabbits, no fluid 'wash-back' is involved in the 'mucus trap' separation mechanisms in these groups (Hume and Sakaguchi 1991).

To our knowledge, the flexibility of the role coprophagy plays as part of the overall digestive strategy in small herbivores is little explored so far, except for rabbits. In rabbits, it was shown that caecotroph production, or the contribution of cecotrophs to overall intake, increased with increasing dietary fibre and decreasing dietary protein concentrations (Fekete and Bokori 1985; Carabaño et al. 1988; García et al. 1995). Fekete and Bokori (1985) actually demonstrated that rabbits ingested a lower proportion of their cecotrophs on low-fibre, high-protein diets. The finding that the excretion patterns of MRT markers indicated less coprophagic incidents in viscachas on the diets higher in protein suggests that a similar mechanism may influence the choice to practice coprophagy in other small herbivores, too.

*6.2.5 Diabetes susceptibility and diets fed in captivity*

The observation that plains viscachas are susceptible to diabetic states when fed energy-dense diets was confirmed in this study. Similar to free-ranging animals investigated by Wenker et al. (2007), urine tested negative for glucose on forage-only diets (Exp1A, Exp2A/C), but glucosuria was evident in individual animals on energy-dense diets (Exp1B, Exp2B). The serum glucose in all animals, and fructosamine levels in Exp1, were within the reference range (4.7-11.2 mmol $l^{-1}$ for glucose and 161-297 µmol $l^{-1}$ for fructosamine) determined in free-ranging plains viscachas (Wenker et al. 2007). In contrast, fructosamine levels in Exp2 were above these levels, for both the forage-only and the concentrate diet, indicating that repeated measures of the same individuals may yield more important information than a comparison with reference ranges. In Exp2B, the extremely wide range of urinary glucose as well as the high standard deviation for serum glucose and fructosamine underline a large inter-individual variety in the response to energy-dense diets. In sand rats (*Psammomys obesus*), another rodent species with a high susceptibility to diabetes and cataract formation, individual differences in susceptibility to the problem due to hereditary factors have been demonstrated (Kalman et al. 1993; Walder et al. 2000) and might also play a role in plains viscachas.

Faecal nitrogen (FN) in free-ranging viscachas ranged between 1.2 and 1.9 %DM (Branch et al. 1994), with data from forage-only diets of Exp1 and 2 well within this range, the concentrate diet in Exp2B at the upper end of it, and both the lucerne hay diet of Exp3 and the concentrate diet in Exp1B well above it. Because FN is related to the digestibility of the diet in herbivores (Steuer et al. 2014; Gálvez-Cerón et al. 2015) as also evident in the data of the plains viscacha of this study, this comparison indicates that the concentrate diets of this study are more digestible than the diets plains viscachas probably have adapted to over evolution. The relevance of maintaining rodents susceptible to diabetic conditions (incl. cataract formation) on high-fibre diets without concentrates has been repeatedly stated with respect not only to viscachas (Gull et al. 2009; Wenker et al. 2009) but also degus (Edwards 2009), tuco-tucos (*Ctenomys talarum*) (Wise et al. 1972), agoutis (*Dasyprocta* spp.) (McWilliams 2009), or sand rats (Kalman et al. 1993).

*6.2.6 Comparative digestive efficiency for nutrients and minerals*

In theory, it could be expected that in animals that practice coprophagy, the major effect of which is the re-ingestion of microbial matter, should have particularly high apparent digestion coefficients for those nutrients that are abundant in microbes, such as protein, lipids, and phosphorus. The comparisons in this study do not suggest systematic differences in this respect between the horse and the coprophageous mammals. Similarly, no differences in metabolic faecal nitrogen losses could be demonstrated in a survey of various mammalian digestion strategies including coprophageous and non-coprophageous hindgut fermenters and ruminant and non-ruminant foregut fermenters (Schwarm et al. 2009), and the protein digestibility also did not differ noticeably between foregut-fermenting hippopotamuses and large hindgut fermenters (Schwarm et al. 2006) or between various hindgut-fermenting suids and foregut-fermenting tayassuids (Clauss et al. 2008). On the one hand, there really might be no differences in the apparent digestibility of microbe-related nutrients between the digestion strategies. This hypothesis still requires a theoretical explanation, but emphasises that the focus in comparative digestive physiology is more fruitfully placed on considerations of fibre digestion and intake limitation (Justice and Smith 1992; Clauss et al. 2010a; Clauss et al. 2015). On the other hand, these differences in the apparent digestibility, i.e. in the true digestibility and in the endogenous/metabolic faecal losses, of microbe-related nutrients might be too delicate to be reflected in broad comparative approaches that collate data from various sources (see chapter 6.1.1), and would have to be investigated in carefully designed comparative feeding experiments.

Another potential assumption on differences between horses and the smaller herbivores relates to theories on the influence of body mass on herbivore digestive capacity (Demment and Van Soest 1985). The fact that in horses, an increase in dietary crude fibre does not affect organic matter digestibility as much as in rabbits or guinea pigs (see Fig. 1.3), could be explained by the generally longer particle mean retention times of horses at 23-34 h (Clauss et al. 2014) as compared to 15 h in rabbits and 18 h in guinea pigs (Franz et al. 2011a). The absence of a difference between horses and plains viscachas (Fig. 2.5) could then partially be explained by the similarity of particle mean retention times in the latter (23-30 h, Table 2.3). The combination of these long retention times and the higher degree of ingesta particle size reduction in plains viscachas as compared to horses (Fritz et al. 2009) might also explain the level of methane production in this species, which is higher than expected for the viscacha's body mass based on comparative data from horses, rabbits and guinea pigs (Franz et al. 2011b). Although the plains viscacha has a higher body mass than rabbits and guinea pigs, the difference in body size to horses evidently is of a much higher magnitude, indicating that a small body size as such represents no compulsory limitation for the ability to digest fibrous diets, but that many small herbivores might rather have lost the ability to use such diets because the fact that they can often select higher quality diets offered them the opportunity to do so (Clauss et al. 2013).

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